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RESPONSE OF PREDATOR-PREY SYSTEMS TO NUTRIENT ENRICHMENT AND PR--ETC(U)

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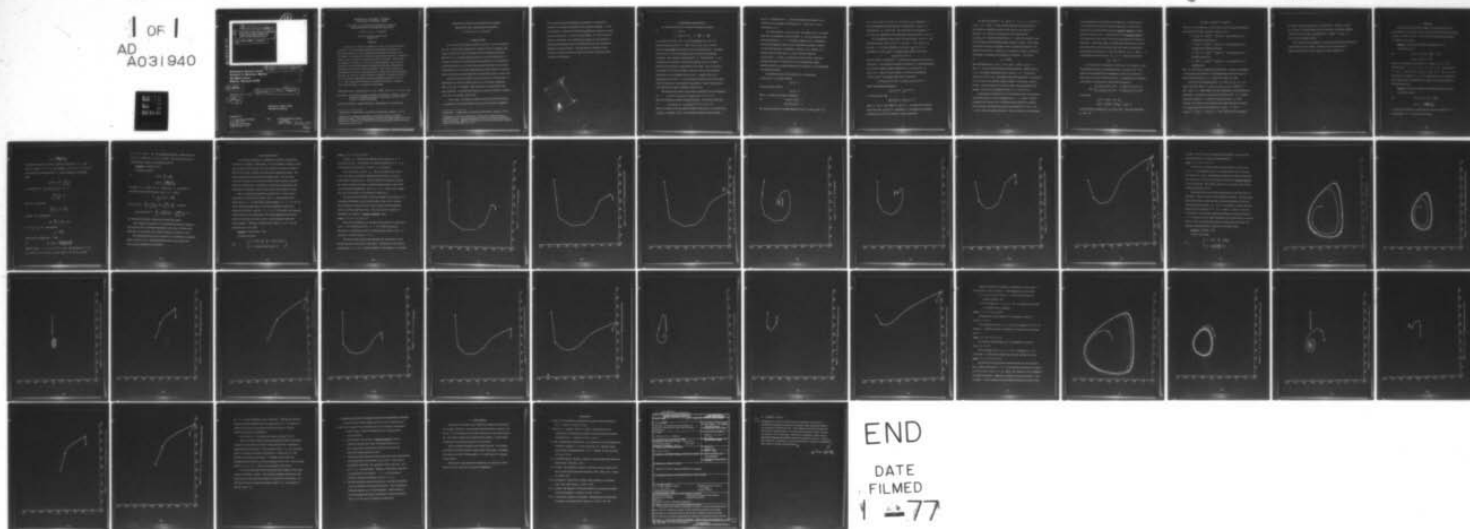
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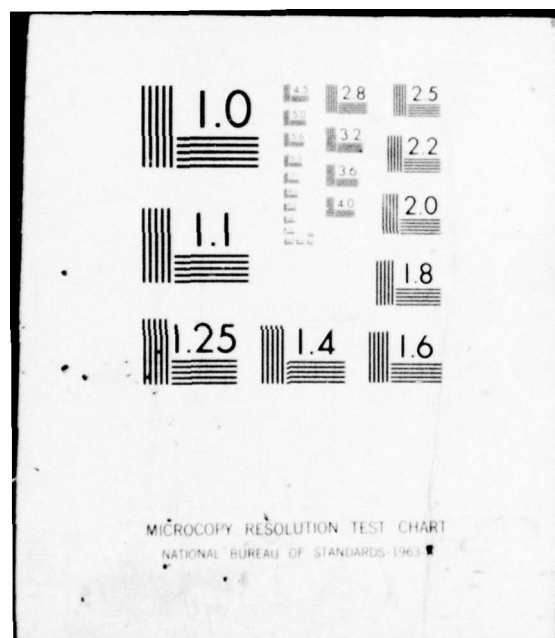
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9 MRC Technical Summary Report #1664

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PROPORTIONAL HARVESTING

10 F. Brauer and A. C. Soudack

Mathematics Research Center  
University of Wisconsin-Madison  
610 Walnut Street  
Madison, Wisconsin 53706

14 MRC-TSR-1664

11 August 1976

(Received July 19, 1976)

15 DAAG29-75-C-0024

12 47 p.

Approved for public release  
Distribution unlimited

Sponsored by

U. S. Army Research Office  
P. O. Box 12211  
Research Triangle Park  
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RESPONSE OF PREDATOR-PREY SYSTEMS TO NUTRIENT  
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F. Brauer<sup>†</sup> and A. C. Soudack<sup>‡</sup>

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ABSTRACT

A predator-prey system is modelled by a pair of ordinary differential equations, and the qualitative effects of prey nutrient enrichment and predator harvesting at a rate proportional to the predator population size are studied. Some theoretical analysis concerning the stability of equilibrium points and the existence of stable limit cycles is included. Three models are examined as examples, and for two of them computer simulations are included to illustrate the changes in qualitative behaviour under nutrient enrichment and increase of harvesting effort. The essential difference between this study and our previous work on constant rate harvesting (Brauer, Soudack, and Jarosch, 1976) is that here, extinction of predators in finite time is impossible although the predator population may tend to zero as  $t \rightarrow \infty$ . Also extinction of predators is much less sensitive to changes of harvesting effort than for constant rate harvesting.

AMS (MOS) Subject Classifications: 34-04, 34A10, 34C05, 69.34, 92-04, 92A15

Key Words: Ecological Modelling, Predator Prey Systems, Stability, Ordinary Nonlinear Differential Equations, Harvesting of Predator-Prey Systems, Computer Simulation

Work Unit Numbers 1 (Applied Analysis) 3 (Applications of Mathematics)

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<sup>†</sup>Department of Mathematics, University of Wisconsin, Madison, U.S.A.

<sup>‡</sup>Department of Electrical Engineering, University of British Columbia, Vancouver, Canada. Research sponsored in part by the United States Army under Contract No. DAAG29-75-C-0024 and in part by the National Research Council of Canada grant #67-3138.



# RESPONSE OF PREDATOR-PREY SYSTEMS TO NUTRIENT ENRICHMENT AND PROPORTIONAL HARVESTING

F. Brauer<sup>†</sup> and A. C. Soudack<sup>‡</sup>

## 1. INTRODUCTION

In a previous study (Brauer, Soudack, Jarosch, 1976) we considered the effect of harvesting predators at a constant rate from a predator-prey system modelled by a pair of nonlinear ordinary differential equations. With the aid of a general analysis applied to specific examples and of computer simulations we demonstrated the possibilities of discontinuities in limiting behaviour of solutions under nutrient enrichment and increases in harvesting rate and of both stabilization and destabilization of systems. These possibilities include extinction of the predator species in finite time.

In many ecological systems it is more natural to study the effect of harvesting at a rate proportional to the size of the predator population. This is the case, for example, when the harvest is proportional to the effort expended, a situation often assumed in models for fisheries management, see, for example, Clark (1974).

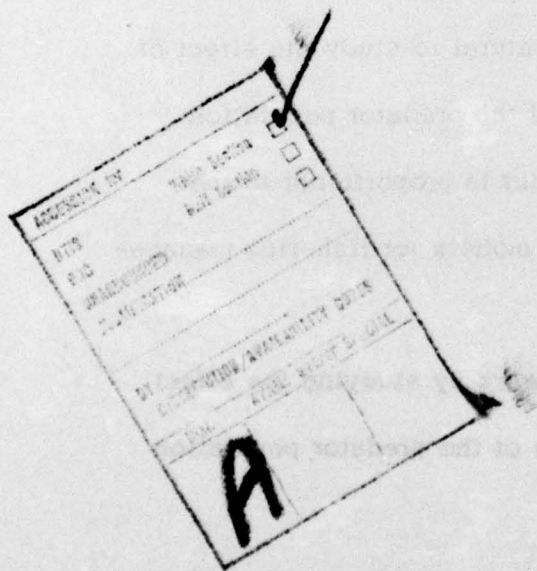
In this paper, we parallel our previous work by studying the effect of harvesting at a rate proportional to the size of the predator population

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<sup>†</sup>Department of Mathematics, University of Wisconsin, Madison, U.S.A.

<sup>‡</sup>Department of Electrical Engineering, University of British Columbia, Vancouver, Canada. Research sponsored in part by the United States Army under Contract No. DAAG29-75-C-0024 and in part by the National Research Council of Canada grant #67-3138.

with a theoretical analysis followed by analysis of some specific examples and computer simulations of two of these examples. It turns out that there are significant differences between the dynamics of proportional harvesting and of constant rate harvesting. We shall draw some specific conclusions, but in general the situation is that response to proportional harvesting is more predictable and much less sensitive to changes in initial conditions. The possibility of extinction of the predators in finite time does not arise in this case, unlike the case of constant rate harvesting.





## 2. THEORETICAL BACKGROUND

We consider the system of ordinary differential equations

$$(1) \quad \begin{aligned} x' &= xf(x, y) \\ y' &= yg(x, y) - Ey, \quad x' = \frac{dx}{dt}, \quad y' = \frac{dy}{dt} \end{aligned}$$

as a model for the sizes  $x(t)$  of a prey population and  $y(t)$  of a predator population at time  $t$ . Here,  $f(x, y)$  and  $g(x, y)$  are the respective per capita growth rates of the two population sizes. Predators are harvested at a time rate proportional to the size of the predator population, with constant of proportionality  $E$ . This parameter  $E$  may be regarded as a measure of the harvesting effort, and it is assumed that the harvesting rate is proportional to this effort. As in our previous work (Brauer 1976, Brauer, Soudack, Jarosch 1976) we assume that the growth rates of the population sizes at time  $t$  depend only on the population sizes at time  $t$ , even though this neglects many factors which could be important for real predator-prey systems. Some of these factors were suggested in (Brauer, Soudack, Jarosch 1976).

The predator-prey nature of the model is expressed by the assumptions

$$(2) \quad f_y(x, y) < 0, \quad g_x(x, y) > 0, \quad g_y(x, y) \leq 0, \quad [x > 0, y > 0]$$

where the subscripts indicate partial derivatives. We assume further that

$$(3) \quad f_x(x, y)g_y(x, y) - f_y(x, y)g_x(x, y) > 0, \quad [x > 0, y > 0]$$

which is satisfied by all the standard models of the form (1) for predator-prey systems, cf. (Brauer, 1976). In the examples which we shall consider,

$g(x, y)$  is independent of  $y$ , which means that the predators do not interfere with one another in obtaining food. In this case, (3) is a consequence of (2).

We shall denote by  $[x(t, E), y(t, E)]$  any solution of (1), to indicate explicitly the dependence on the parameter  $E$ . We are interested in the limiting behaviour as  $t \rightarrow \infty$  of bounded solutions of (1). According to the Poincare-Bendixson theory of two-dimensional autonomous systems of differential equations (Coddington, Levinson, 1955, Chapter 16), a bounded solution either tends to a limit, which we denote by  $[x_\infty(E), y_\infty(E)]$ , or tends to a periodic orbit (limit cycle). Since the only possible limits of solutions of (1) are asymptotically stable equilibrium points, we study the behaviour of solutions of (1) by examining the equilibrium points.

An equilibrium point of the system (1) is an intersection  $[x_\infty(E), y_\infty(E)]$  of the prey isocline

$$f(x, y) = 0$$

and the predator isocline

$$g(x, y) = E,$$

that is, a solution of the pair of equations

$$(4) \quad \begin{aligned} f\{x_\infty(E), y_\infty(E)\} &= 0 \\ g\{x_\infty(E), y_\infty(E)\} &= E. \end{aligned}$$

We assume that there is a unique equilibrium point  $[x_\infty(0), y_\infty(0)]$  for



$E = 0$  with  $x_{\infty}(0) > 0$ ,  $y_{\infty}(0) > 0$ . In view of (2), an increase in  $E$  moves the predator isocline (which is a vertical line if  $g(x, y)$  is independent of  $y$ ) to the right. Thus the effect of an increase in  $E$  is to move the equilibrium to the right along the prey isocline  $f(x, y) = 0$ .

In the examples we shall study, the prey isocline  $f(x, y) = 0$  has a unique maximum, with  $f_x(x, y) > 0$  for small  $x$  and  $f_x(x, y) < 0$  for large  $x$ . It is known (Brauer, 1976) that if  $g_y(x, y) \equiv 0$ , an equilibrium  $[x_{\infty}(E), y_{\infty}(E)]$  is asymptotically stable if and only if

$$f_x\{x_{\infty}(E), y_{\infty}(E)\} < 0.$$

Since the effect of increasing  $E$  is to move the equilibrium to the right, increasing  $E$  may change an unstable equilibrium to a stable equilibrium, but it can not change a stable equilibrium to an unstable one. If  $g_y(x, y) \not\equiv 0$ , then it is known (Brauer, 1976) that an equilibrium  $[x_{\infty}(E), y_{\infty}(E)]$  is asymptotically stable if and only if

$$x_{\infty}(E)f_x\{x_{\infty}(E), y_{\infty}(E)\} + y_{\infty}(E)g_y\{x_{\infty}(E), y_{\infty}(E)\} < 0.$$

Under the additional hypotheses

$$g_{xy}(x, y) \leq 0, \quad f_{xx}(x, y) < 0,$$

it is easy to show that

$$\frac{d}{dx} [xf_x(x, y) + yg_y(x, y)] < 0,$$

where  $x$  and  $y$  are related by  $f(x, y) = 0$ , and from this it follows that in the case  $g_y(x, y) \not\equiv 0$  increasing  $E$  can stabilize an unstable equilibrium but can not destabilize a stable equilibrium.



We define the number  $K$  by  $f(K, 0) = 0$ , or  $K = \infty$  if  $f(x, 0) > 0$  for all  $x > 0$ . Thus  $K$  is the carrying capacity of the prey species - the equilibrium population the prey would obtain in the absence of predators. It is clear from the geometry of the isoclines that  $[x_\infty(E), y_\infty(E)]$  depends continuously on  $E$ , unlike the situation in the case of constant rate harvesting (Brauer, Soudack, Jarosch, 1976), where the equilibrium point can disappear with a consequent extinction of the predators in finite time. However, it is possible to produce a biological catastrophe by harvesting the predators to extinction. If we define

$$(5) \quad E_c = g(K, 0),$$

then the equilibrium for  $E \geq E_c$  is at  $(K, 0)$ , so that  $y_\infty(E_c) = 0$ .

Thus  $E_c$  may be called the critical harvesting effort. Observe that for  $E \geq E_c$  the predator population tends to zero as  $t \rightarrow \infty$  but does not reach zero in finite time. Enrichment of the prey environment, as described by an increase in the carrying capacity (Brauer, 1976; Brauer, Soudack, Jarosch, 1976) will produce an increase in the critical harvesting effort because  $g(K, 0)$  is an increasing function of  $K$ , in view of (2).

In studying real populations, we are interested only in the solutions of (1) which remain in the first quadrant of the  $x - y$  plane. If either population ever becomes zero, the predator-prey system will collapse. For this reason, the equilibrium points of the system (1) at  $(0, 0)$  and at  $(K, 0)$  are of no practical interest. In fact, because of the possibility

of small perturbations and errors in the system (1), we should require that solutions do not come too close to either axis. It was for this reason that we introduced the concept of practical stability in (Brauer, Soudack, Jarosch, 1976). A system is said to be practically stable if its solution orbit never comes closer than some preassigned distance to either axis. In the same spirit, we should define the practical critical harvesting effort as the harvesting effort which moves the equilibrium along the prey isocline not to  $(K, 0)$  but rather to  $(x_\epsilon, \epsilon)$ , where  $\epsilon$  is a preassigned safety margin and  $f(x_\epsilon, \epsilon) = 0$ . Thus we might define

$$E_{pc} = g(x_\epsilon, \epsilon).$$

It is well-known (Coddington and Levinson, 1955, Chapter 15) that the qualitative nature of an equilibrium point  $[x_\infty(E), y_\infty(E)]$  of the system (1) is determined by the eigenvalues of the matrix obtained by linearizing the system (1) about this point. A straightforward calculation, using Taylor's theorem and (4), shows that this matrix is

$$A(E) = \begin{bmatrix} x_\infty(E)f_x\{x_\infty(E), y_\infty(E)\} & x_\infty(E)f_y\{x_\infty(E), y_\infty(E)\} \\ y_\infty(E)g_x\{x_\infty(E), y_\infty(E)\} & y_\infty(E)g_y\{x_\infty(E), y_\infty(E)\} \end{bmatrix}.$$

If we define

$$\Delta_1(E) = \text{tr } A(E) = xf_x + yg_y$$

$$\Delta_2(E) = \det A(E) = xy(f_xg_y - f_yg_x) > 0,$$

with all functions evaluated at  $[x_\infty(E), y_\infty(E)]$ , then the eigenvalues of  $A(E)$  are



$$\frac{1}{2} \{ \Delta_1(E) \pm [ \{ \Delta_1(E) \}^2 - 4 \Delta_2(E) ]^{\frac{1}{2}} \}.$$

We have four possibilities, just as in the case of constant rate harvesting examined in (Brauer, Soudack, Jarosch, 1976).

1. If  $\Delta_1(E) < 0$ ,  $\{ \Delta_1(E) \}^2 - 4 \Delta_2(E) \geq 0$ , the equilibrium is an asymptotically stable node.
2. If  $\Delta_1(E) < 0$ ,  $\{ \Delta_1(E) \}^2 - 4 \Delta_2(E) < 0$ , the equilibrium is an asymptotically stable spiral point.
3. If  $\Delta_1(E) > 0$ ,  $\{ \Delta_1(E) \}^2 - 4 \Delta_2(E) < 0$ , the equilibrium is an unstable spiral point.
4. If  $\Delta_1(E) > 0$ ,  $\{ \Delta_1(E) \}^2 - 4 \Delta_2(E) \geq 0$ , the equilibrium is an unstable node.

Also, as in the case of constant rate harvesting, a theorem of Kalmogorov (1936) assures the existence of an asymptotically stable limit cycle in the first quadrant of the  $x - y$  plane in the latter two cases.

For the critical harvesting effort  $E_c$ , since  $y_\infty(E_c) = 0$ , it is easy to see that  $\Delta_1(E_c) = x_\infty(E_c) f_x \{ x_\infty(E_c), y_\infty(E_c) \} = K f_x(K, 0) < 0$  and  $\Delta_2(E_c) = 0$ , which implies that the equilibrium is an asymptotically stable node. In addition to the critical harvesting effort  $E_c$  for which the system collapses, we define the harvesting effort  $E_s$  which stabilizes the system in the sense that the stable limit cycle collapses to a stable spiral point, characterized by  $\Delta_1(E_s) = 0$ . Since  $\{ \Delta_1(E_s) \}^2 - 4 \Delta_2(E_s) = -4 \Delta_2(E_s) < 0$ , this transition from an unstable

to a stable system always occurs at a spiral point. Further, we could give a name to the harvesting effort which produces a transition between a spiral point and a node, characterized by  $\{\Delta_1(E)\}^2 - 4\Delta_2(E) = 0$ . This will not be explored further.

Now consider some examples to indicate how the foregoing theoretical considerations may be applied, as well as some numerical data to suggest aspects which can not readily be treated analytically.

### 3. EXAMPLES

In this section we apply the results of the preceding section to three examples of biological interest - the same three examples considered in (Brauer, Soudack, Jarosch, 1976) except for order and the difference in the mode of harvesting.

Example 1: Ivlev-type interaction (Rosenzweig, 1971).

Consider the choice

$$(6) \quad \begin{aligned} f(x, y) &= r(1 - x/K) - \frac{by}{x} (1 - e^{-cx}) \\ g(x, y) &= s(e^{-cJ} - e^{-cx}) . \end{aligned}$$

It follows immediately from (5) that  $E_c = g(K, 0) = s(e^{-cJ} - e^{-cK})$ .

With the values  $r = 2$ ,  $s = 1$ ,  $b = 1$ ,  $c = 0.1$ ,  $J = 20$ , we find that for  $K = 25$ ,  $E_c = 0.053$ ; for  $K = 40$ ,  $E_c = 0.117$ ; for  $K = 60$ ,  $E_c = 0.132$ .

The analytic calculation of  $E_s$  is so complicated as to be impractical.

This example will be examined more closely in the numerical study in the following section.

Example 2: Michaelis-Menten type interaction (Holling, 1965).

Consider the choice

$$(7) \quad \begin{aligned} f(x, y) &= r(1 - x/K) - \frac{y}{x + A} \\ g(x, y) &= \frac{sA(x - J)}{(J + A)(x + A)} . \end{aligned}$$

To assure the existence of an equilibrium in the first quadrant for  $E = 0$  we must have  $K > J$ , and from (5) we obtain



$$E_c = \frac{sA(K - J)}{(J + A)(K + A)} .$$

We have shown (Brauer, Soudack, Jarosch, 1976) that for  $E = 0$  the system is stable if  $K < A + 2J$  and unstable if  $K > A + 2J$ . If  $K > A + 2J$ , we calculate the harvesting effort  $E_s$  which stabilizes it as follows:

Since

$$f_x(x, y) = -\frac{r}{K} + \frac{y}{(x + A)^2} ,$$

$E_s$  corresponds to  $f_x\{x_\infty(E_s), y_\infty(E_s)\} = 0$ , or

$$\frac{y_\infty}{(x_\infty + A)^2} = \frac{r}{K} .$$

But from (7) we see that

$$\frac{y_\infty}{x_\infty + A} = r\left(1 - \frac{x_\infty}{K}\right) ,$$

and thus  $E_s$  corresponds to

$$r\left(1 - \frac{x_\infty}{K}\right) = \frac{r}{K}(x_\infty + A) ,$$

or  $K - x_\infty = x_\infty + A$ , with solution

$$x_\infty = \frac{K - A}{2} .$$

If this value is greater than  $J$ , then

$$(8) \quad E_s = g(x_\infty) = \frac{sA(K - A - 2J)}{(J + A)(K + A)} .$$

With the values  $r = 2$ ,  $s = 1$ ,  $A = 10$ ,  $J = 20$ , we find that for  $K = 25$ ,

$E_c = 0.047$ ; for  $K = 40$ ,  $E_c = 0.133$ ; and for  $K = 60$ ,  $E_c = 0.190$ .

For  $K = 25$  and  $K = 40$ , the unharvested system is stable and there is no  $E_s$ , while for  $K = 60$ ,  $E_s = 0.048$ . This example will also be examined more closely in the following section.

Example 3: (O'Brien, 1974).

Consider the choice

$$(9) \quad f(x, y) = \frac{R}{x} - \frac{y}{x + A}$$

$$g(x, y) = \frac{sA(x - J)}{(J + A)(x + A)}$$

for which  $K = \infty$ . Since  $K = \infty$ , there is no  $E_c$ , but there is a harvesting effort which will make  $x_\infty(E) = \infty$ , namely

$$E = \lim_{x \rightarrow \infty} g(x, y) = \frac{sA}{J + A}.$$

From  $f_x(x, y) = -\frac{R}{x^2} + \frac{y}{(x + A)^2}$  and  $\frac{y_\infty}{x_\infty + A} = \frac{R}{x_\infty}$ , we obtain

$$f_x\{x_\infty(E), y_\infty(E)\} = -\frac{R}{x_\infty^2} + \frac{R}{x_\infty(x_\infty + A)} = -\frac{RA}{x_\infty^2(x_\infty + A)} < 0,$$

and therefore the system is stable for all harvesting efforts.

This completes the analysis for proportional harvesting of predator-prey systems and is a parallel development to the case of constant-rate harvesting of our previous paper (Brauer, Soudack and Jarosch, 1976).

The following section gives the results of a comprehensive simulation study of models 1 and 2, and should give the reader some insight into the qualitative behaviour of the systems.

#### 4. SIMULATION STUDY

For illustrative purposes, comprehensive simulation studies have been made on Example 1 (Rosenzweig, 1971) and Example 2 (Holling, 1965). The simulations were carried out on the University of British Columbia's IBM 370/168 using a variable-step Runge-Kutta integration routine. The figures presented in this section are computer plots. The piecewise linearity of the plots is due to the plot routine which connects computed points by straight lines. In actuality, as the step size approaches zero, these plots will approach smooth curves with no discontinuity in slope.

The two parameters available for variation are  $K$ , which can be increased by increasing prey nutrient, and  $E$ , the harvesting effort. Three values of  $K$  are considered in both examples, i.e.  $K = 25, 40, 60$  which correspond respectively to the cases exhibiting a stable node, stable spiral and limit cycle for  $E = 0$ . As  $E$  is increased, the approach of the trajectory to the equilibrium point is not dependent on the initial states of the system and hence, neither is the biological "extinction" of the predators. Therefore, arbitrary initial states of  $(x, y) = (30, 30)$  have been used in all cases.

Example 1: (Rosenzweig, 1971).

Consider the system

$$(10) \quad \left\{ \begin{array}{l} x' = x \left\{ 2 \left( 1 - \frac{x}{K} \right) - \frac{y}{x} [1 - \exp(-0.1x)] \right\} \\ y' = y [ \exp(-2) - \exp(-0.1x) - E ] \end{array} \right\}.$$



Case 1 ( $K = 25, 0.0 \leq E \leq 0.06$ )

Figures 1, 2, 3 indicate the behaviour of the system as  $E$  is increased from zero. As predicted, the stable equilibrium for  $E = 0$  is a node which tends toward the  $x$ -axis as  $E$  is increased.

From the previous section,  $E_c$ , the critical harvesting effort is 0.053, the value for which the equilibrium point reaches  $(K, 0)$  and mathematical collapse occurs. The key difference in behaviour between this system and that subjected to constant rate harvesting is that in this case the trajectory approaches  $(K, 0)$  as  $t \rightarrow \infty$ , while in the constant rate case, the predators go to extinction in finite time.

The conclusion to be drawn is that the collapse of the system due to proportional harvesting is less sensitive than in the case for constant rate harvesting, and hence we have ample warning that the harvesting effort is reaching dangerous levels. As in the case for constant rate harvesting, the concept of "practical stability" holds.

Case 2 ( $K = 40, 0.0 \leq E \leq 0.13$ )

This case corresponds to an increase in prey nutrient as compared to Case 1. The equilibrium point for  $E = 0$  is a stable spiral point, indicating the destabilizing effect of increasing prey nutrient. As  $E$  is increased, we obtain Figures 4, 5, 6, 7.

The above figures indicate the transition from spiral point to node and the approach of this node to the  $x$ -axis. Calculations in the previous section yield  $E_c = 0.117$ , and hence Figure 7 is equivalent to a biological

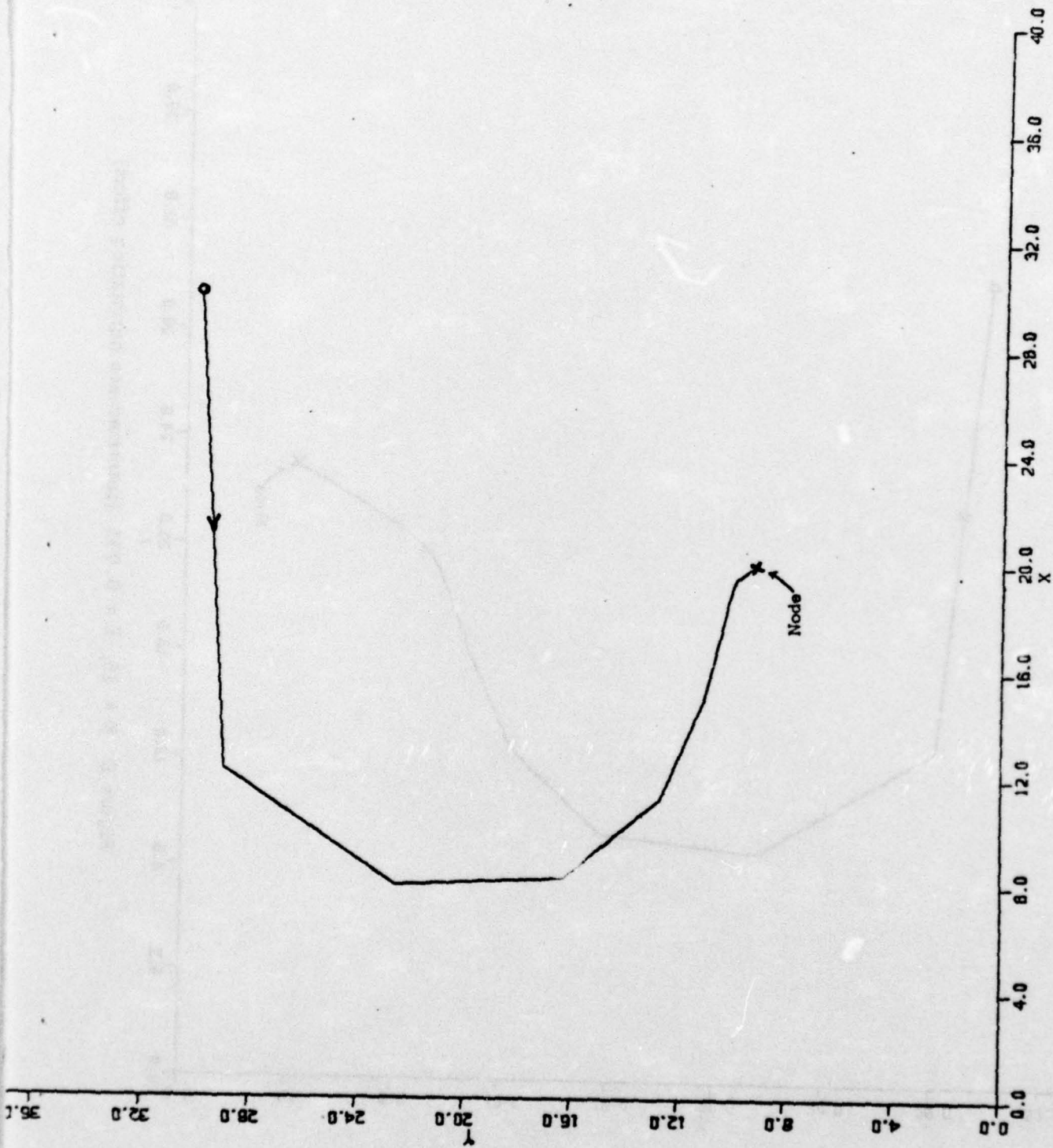


Figure 1  $K = 25$ ,  $E = 0.0$  (no harvesting)



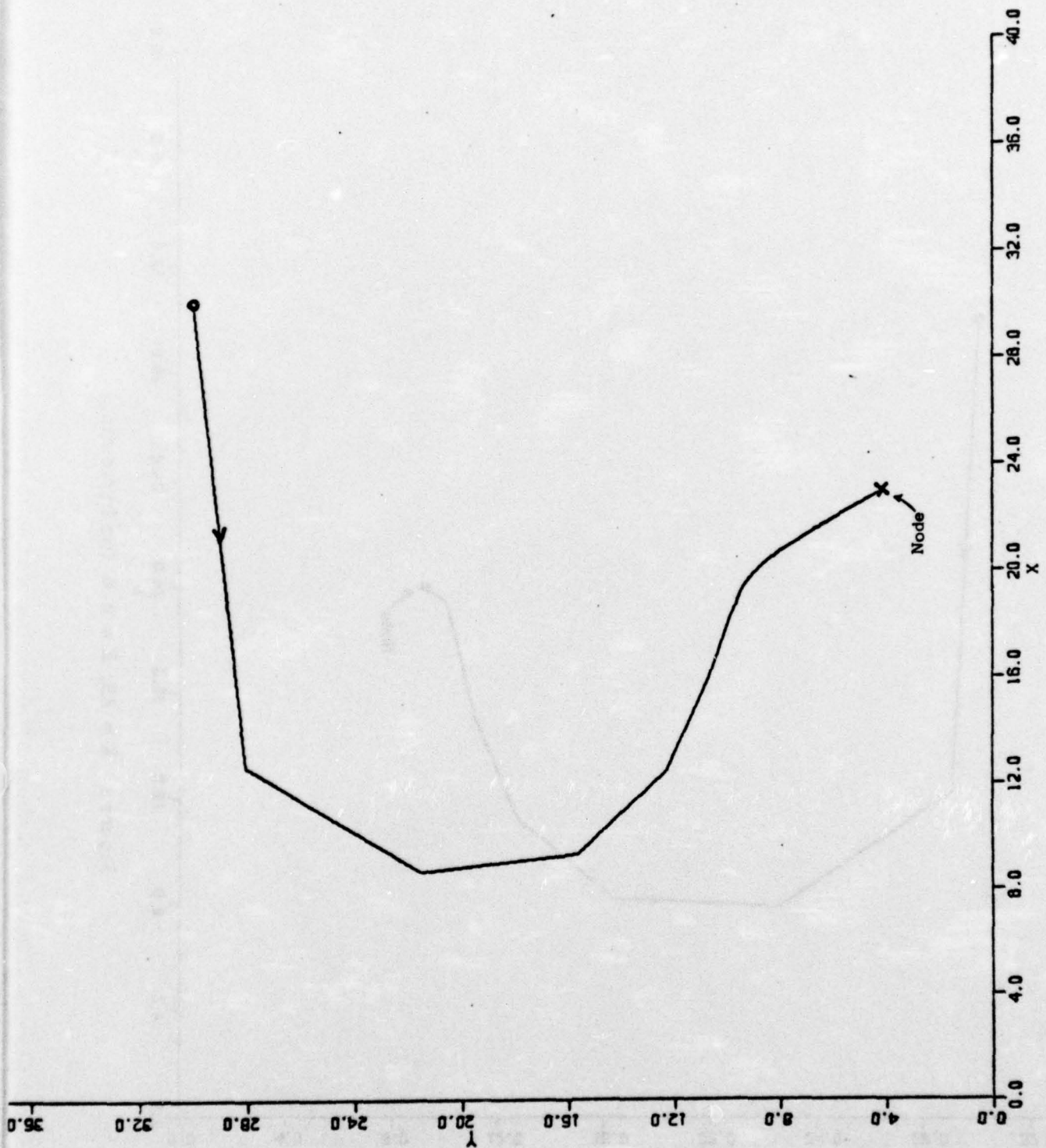


Figure 2  $K = 25$ ,  $E = 0.035$  (intermediate harvesting effort)

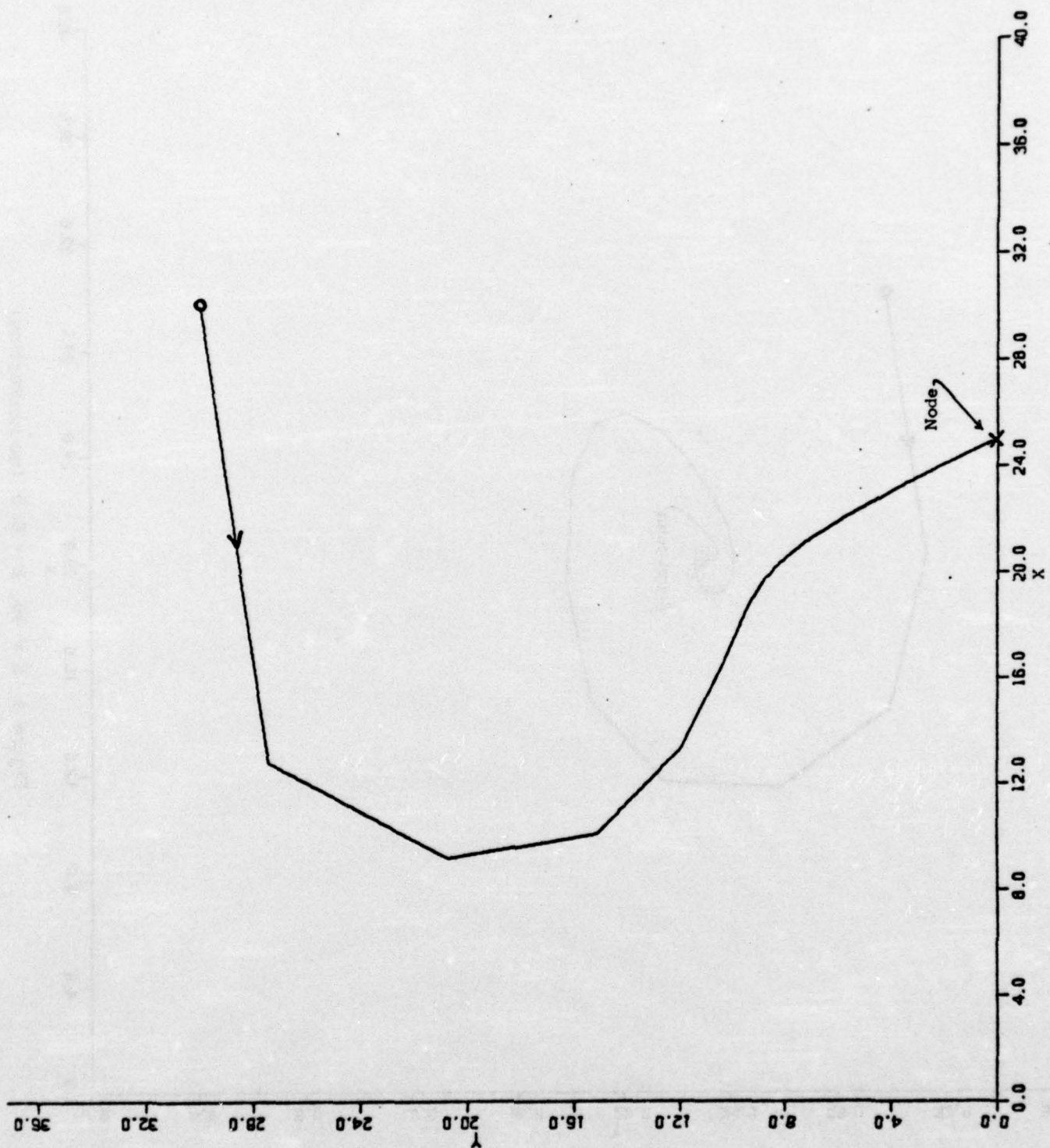


Figure 3  $K = 25$ ,  $E = 0.06$  (harvesting to predator extinction)

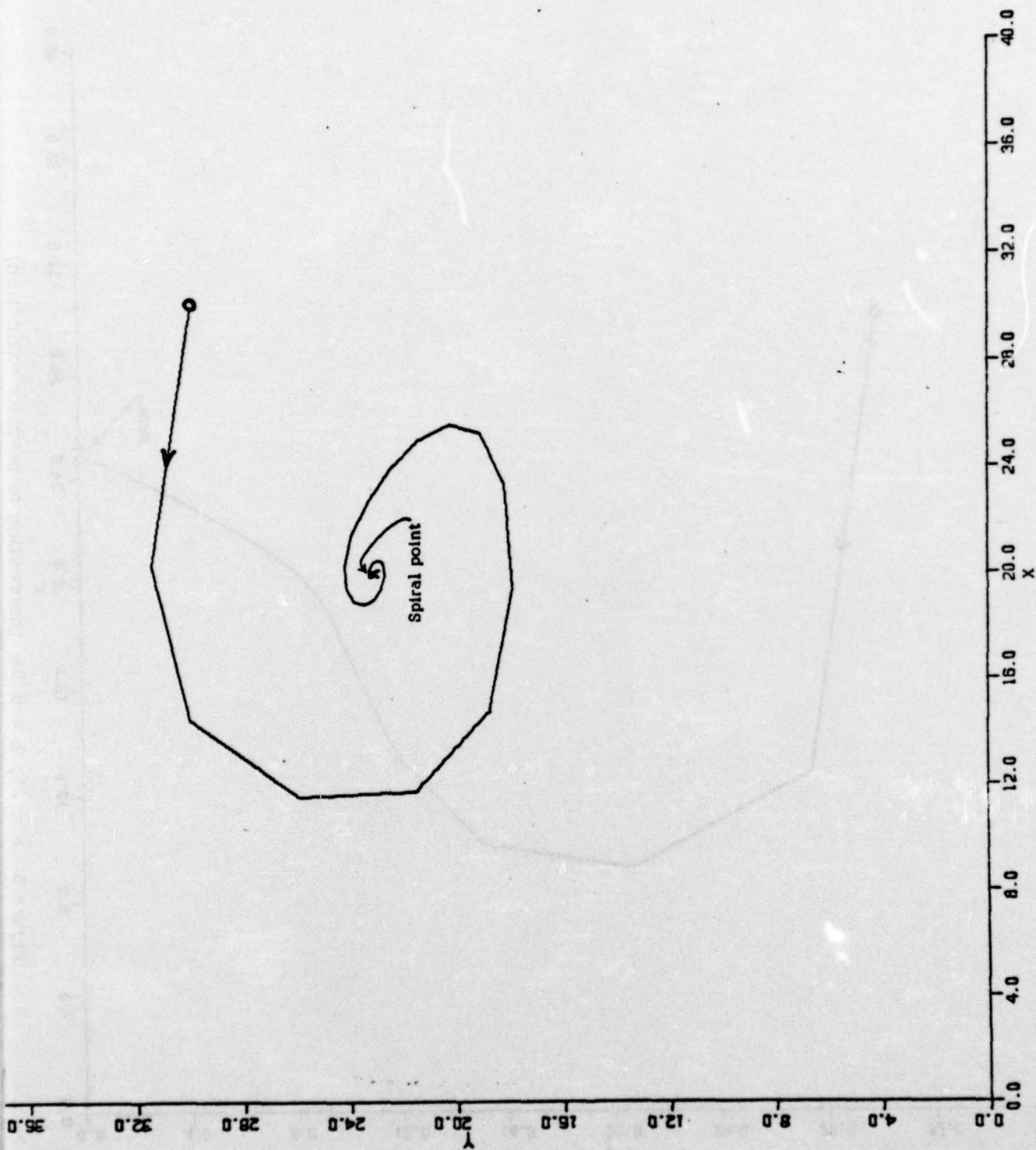


Figure 4  $K = 40$ ,  $E = 0.0$  (no harvesting)



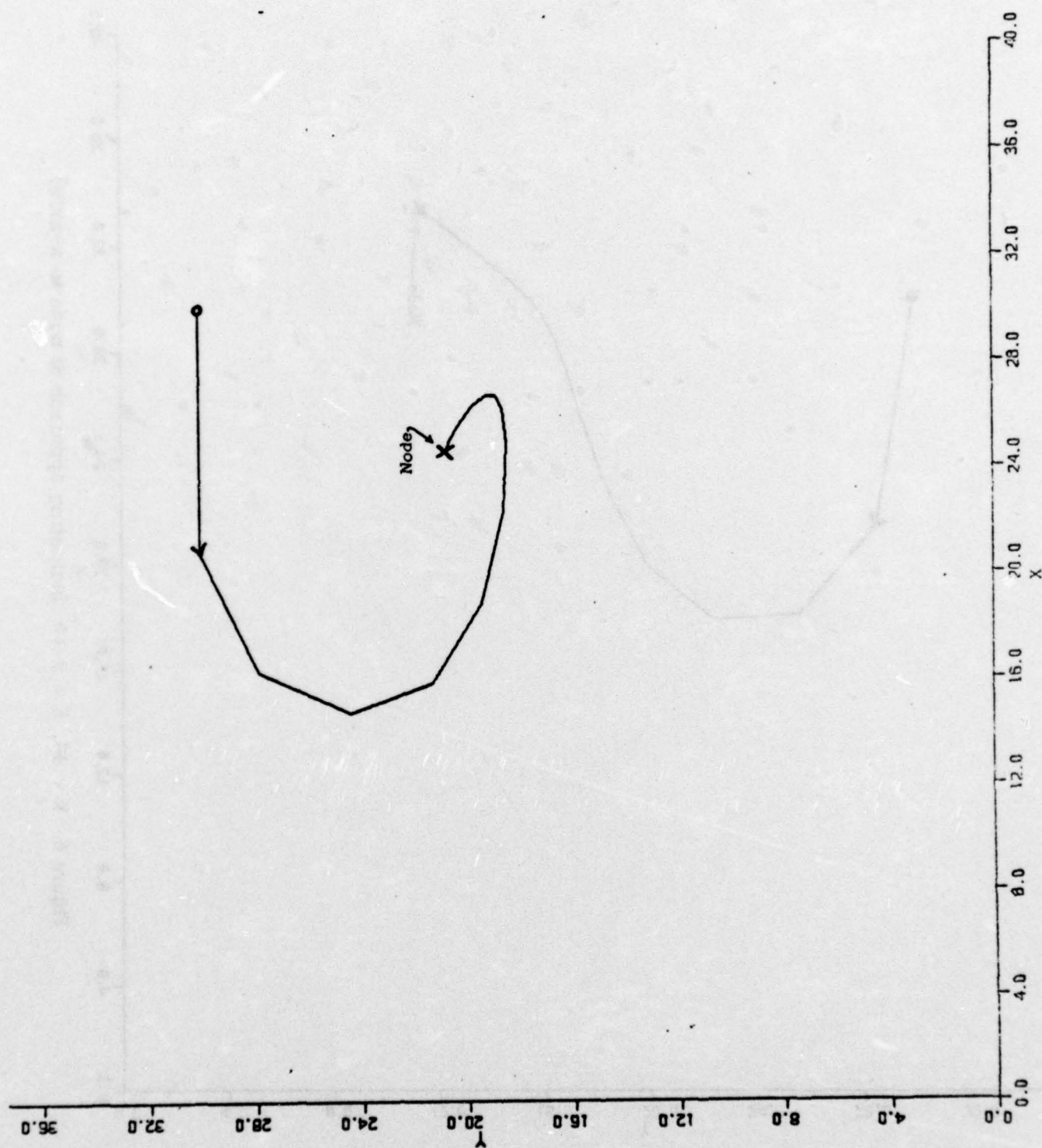


Figure 5  $K = 40$ ,  $E = 0.05$  (harvesting to transition from spiral to node)

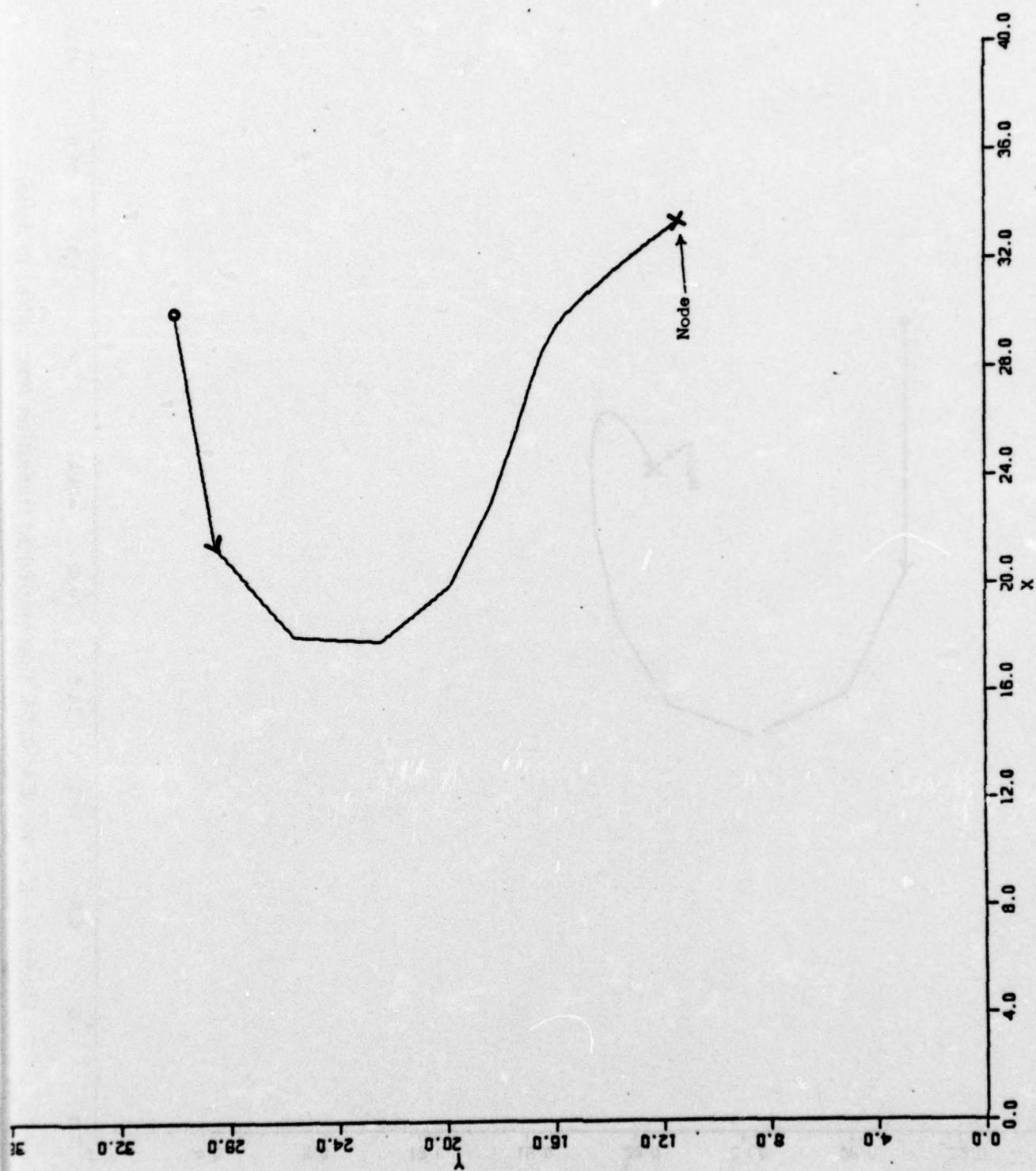


Figure 6  $K = 40$ ,  $E = 0.10$  Indicating approach of node to x-axis)



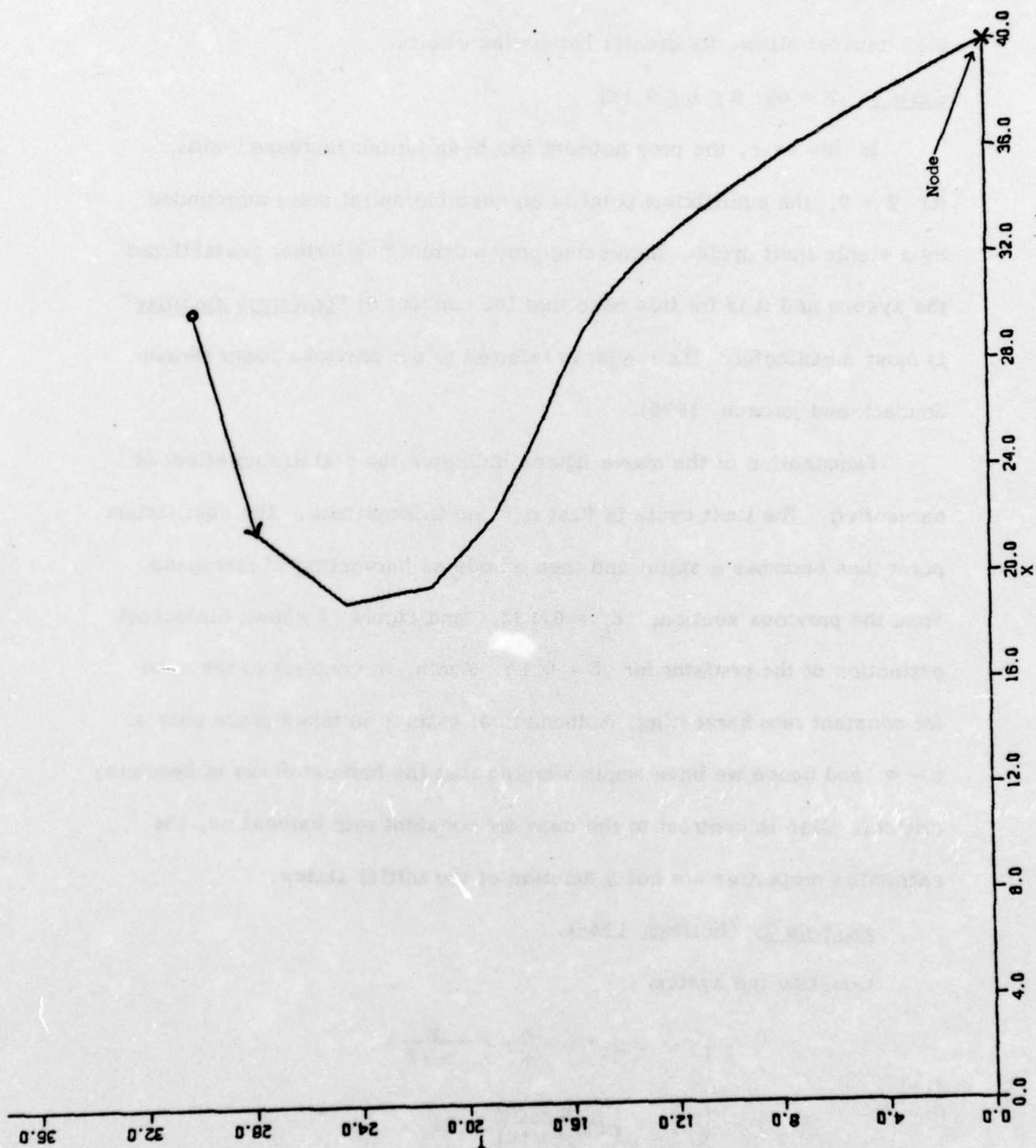


Figure 7  $K = 40$ ,  $E = 0.13$  (harvesting to predator extinction)

collapse. As in the case for constant rate harvesting, increase in the prey nutrient allows for greater harvesting efforts.

Case 3 ( $K = 60, 0 \leq E \leq 0.15$ )

In this case, the prey nutrient has been further increased until, for  $E = 0$ , the equilibrium point is an unstable spiral point surrounded by a stable limit cycle. Increasing prey nutrient has further destabilized the system and it is for this case that the concept of "practical stability" is most meaningful. The reader is referred to our previous paper (Brauer, Soudack and Jarosch, 1976).

Examination of the above figures indicates the stabilizing effect of harvesting. The limit cycle is first reduced in amplitude. The equilibrium point then becomes a spiral and then a node as harvesting is increased. From the previous section,  $E_c = 0.132$ , and Figure 12 shows biological extinction of the predator for  $E = 0.15$ . Again, in contrast to the case for constant rate harvesting, mathematical extinction takes place only as  $t \rightarrow \infty$  and hence we have ample warning that the harvest effort is becoming critical. Also in contrast to the case for constant rate harvesting, the extinction properties are not a function of the initial states.

Example 2: (Holling, 1965).

Consider the system

$$(11) \quad \begin{cases} x' = x \left\{ 2 \left( 1 - \frac{x}{K} \right) - \frac{y}{x+10} \right\} \\ y' = y \left\{ \frac{(x-20)}{3(x+10)} - E \right\} \end{cases}$$

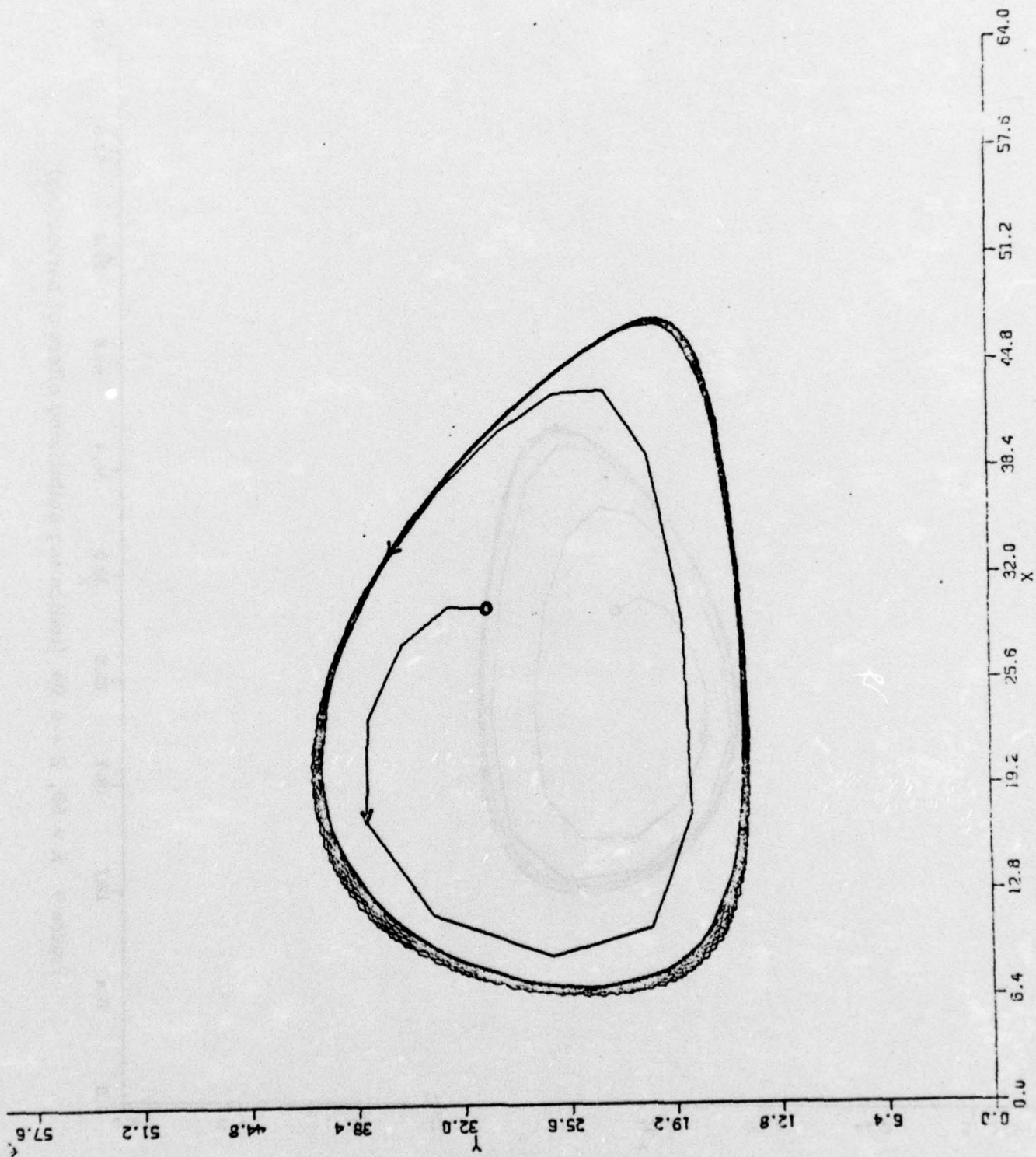


Figure 8  $K = 60$ ,  $E = 0.0$  (no harvesting)





Figure 9  $K = 60$ ,  $E = 0.04$  (indicating stabilizing effect of harvesting)



Figure 10  $K = 60$ ,  $E = 0.07$  (transition of limit cycle to spiral point)

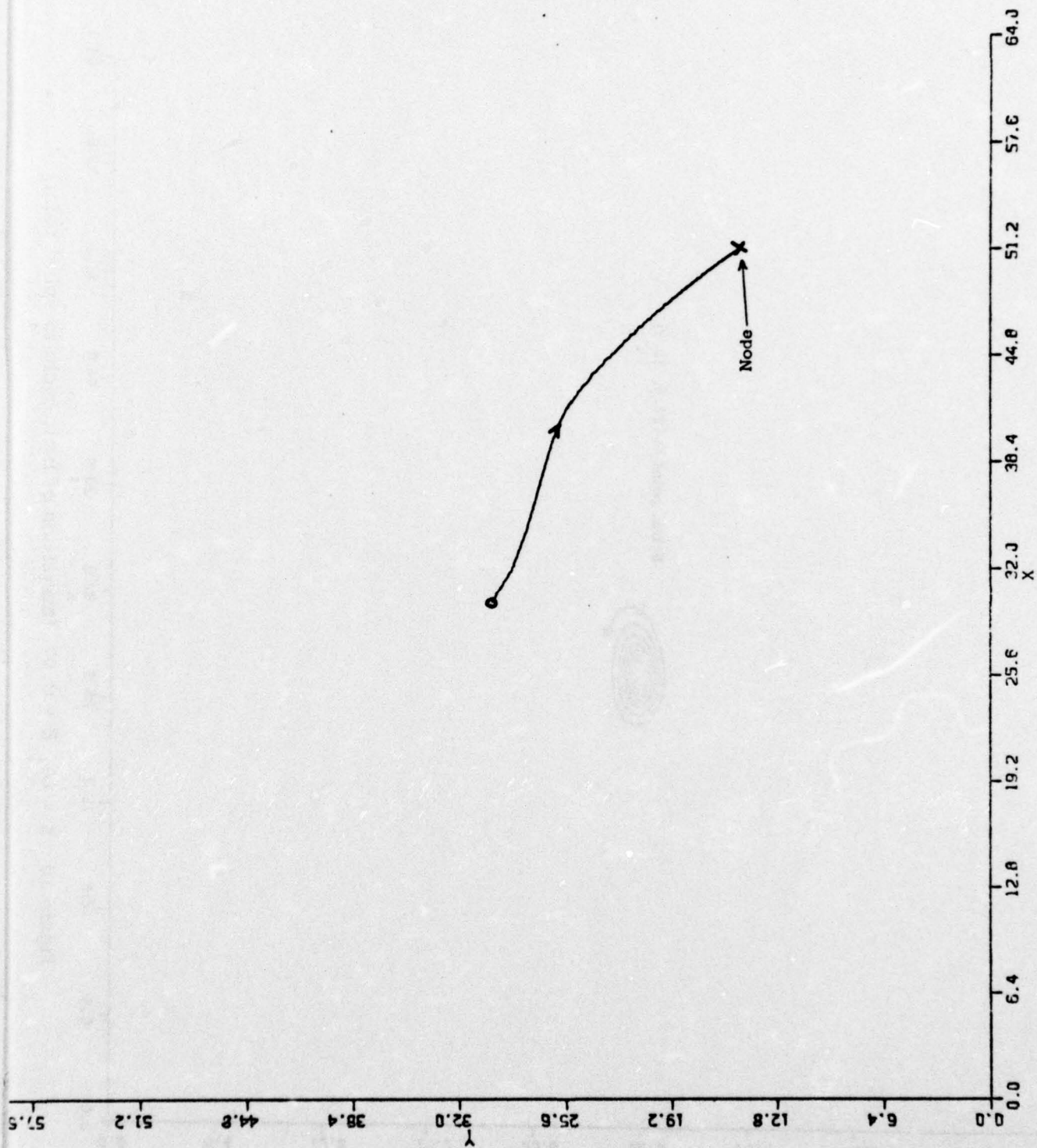


Figure 11  $K = 60$ ,  $E = 0.13$  (indicating approach of node to x-axis)



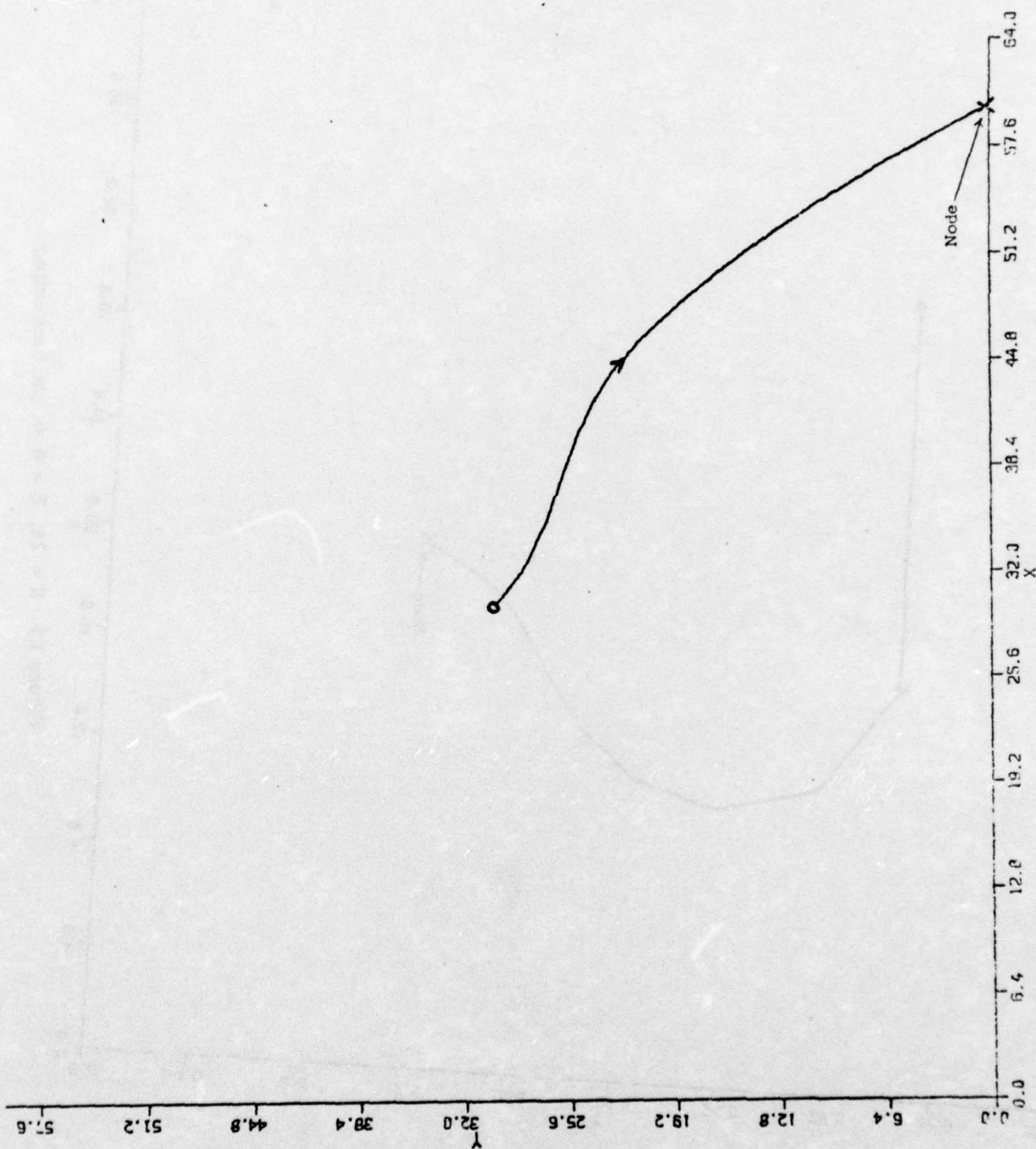


Figure 12  $K = 60$   $F = 0.15$  (harvesting to predator extinction)

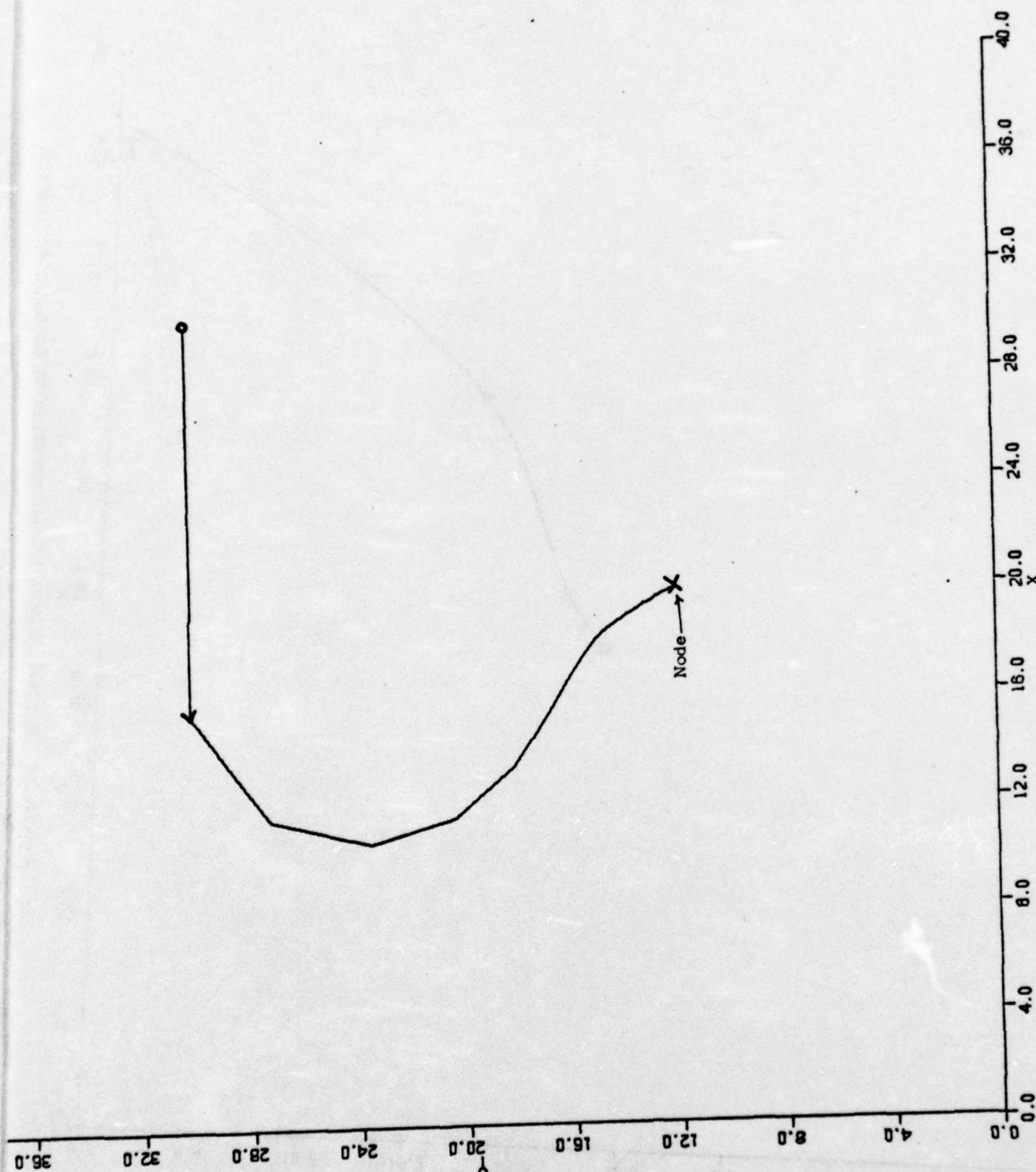


Figure 13  $K = 25$ ,  $E = 0.0$  (no harvesting)

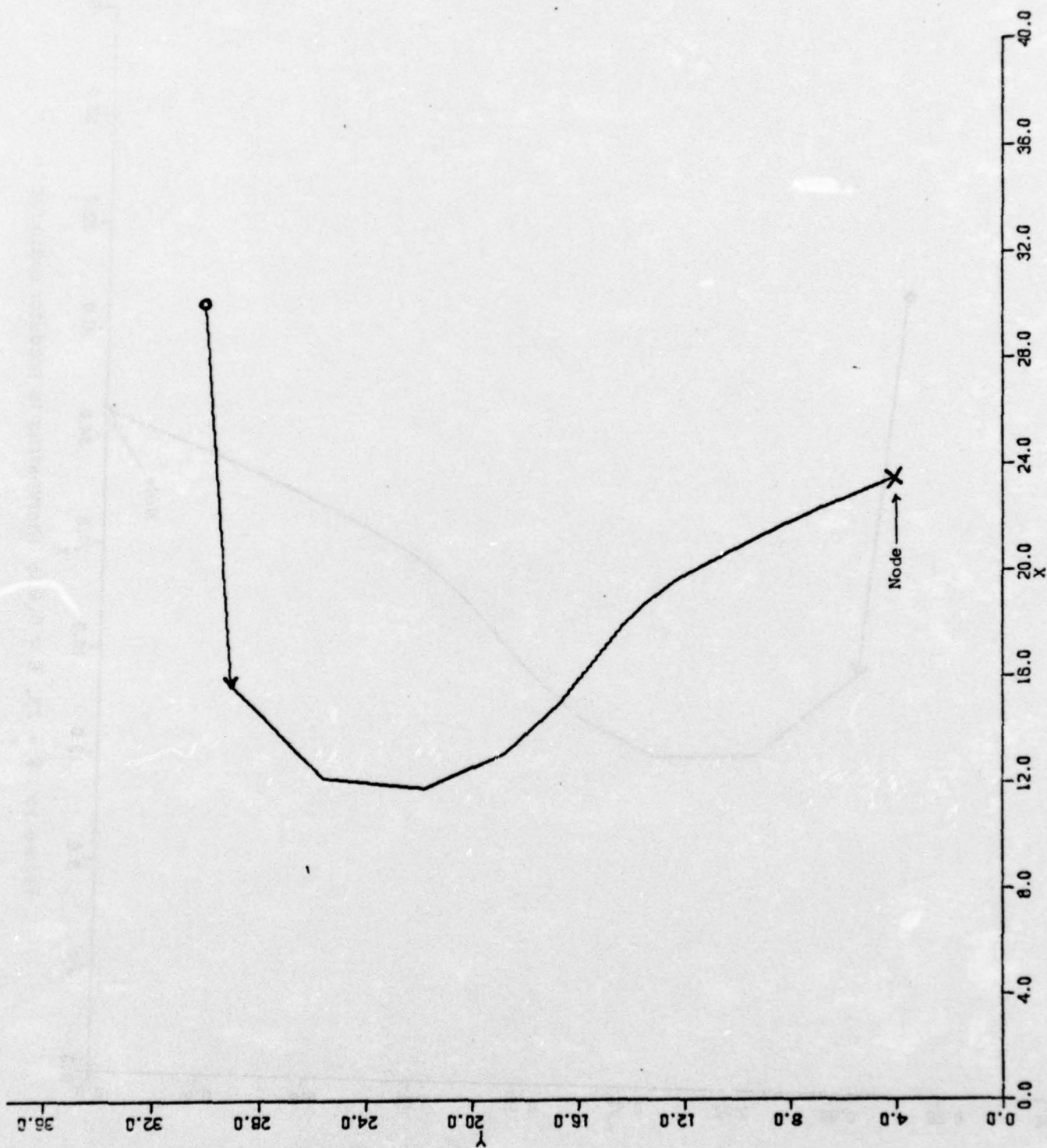


Figure 14  $K = 25$ ,  $E = 0.035$  (intermediate harvesting effort)



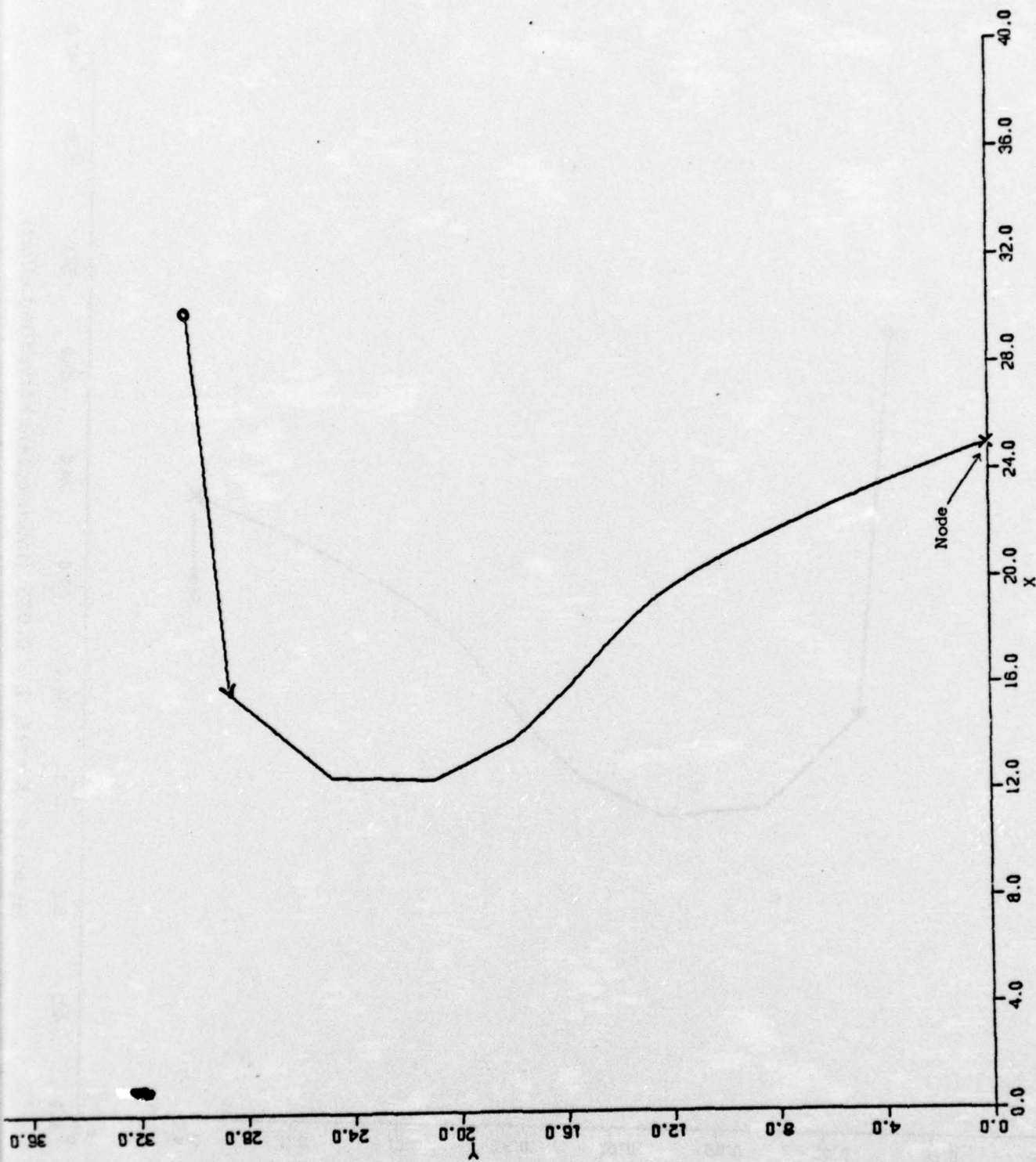


Figure 15  $K = 25$ ,  $E = 0.055$  (harvesting to predator extinction)

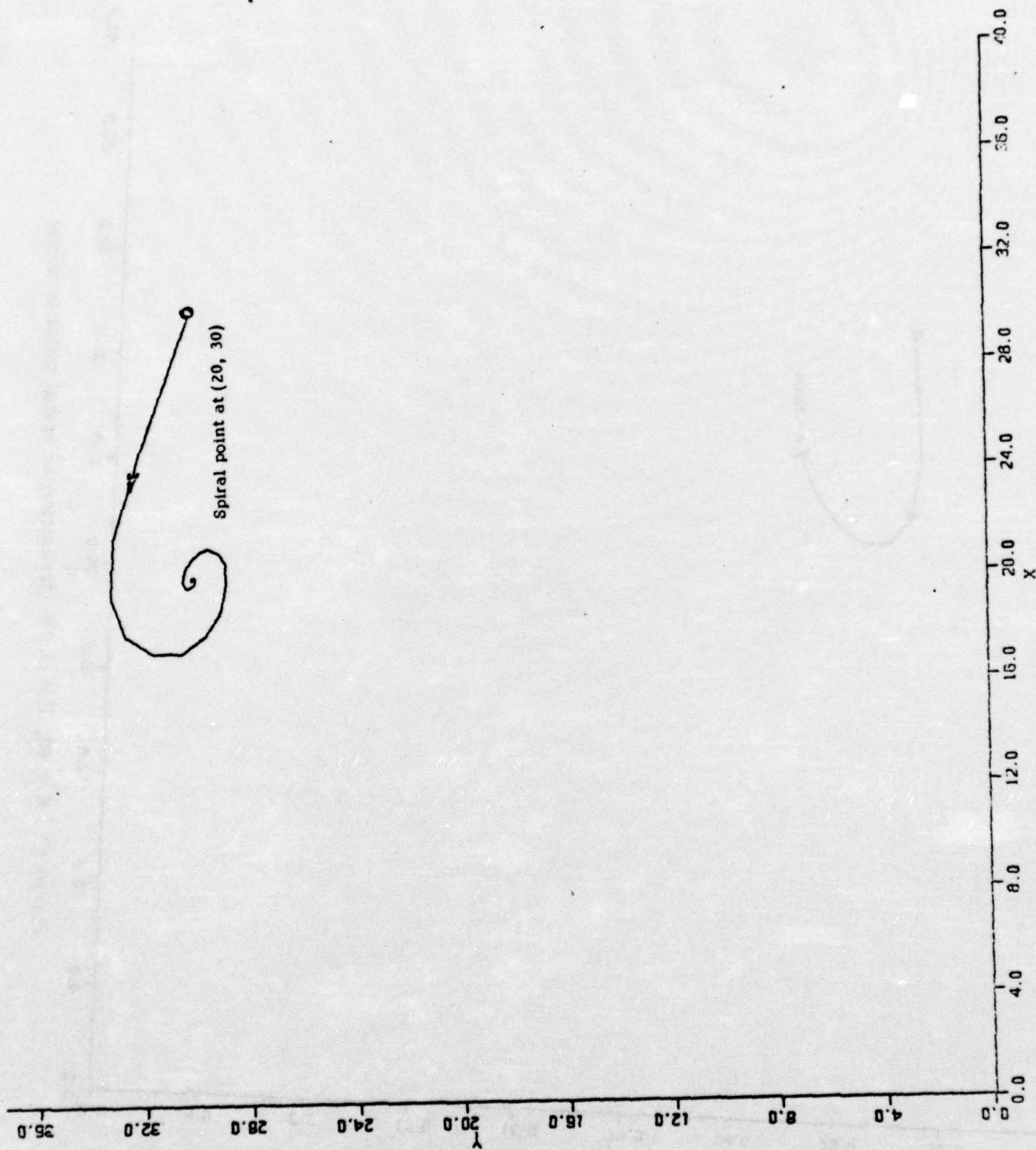


Figure 16  $K = 40$ .  $E = 0.0$  (no harvesting)

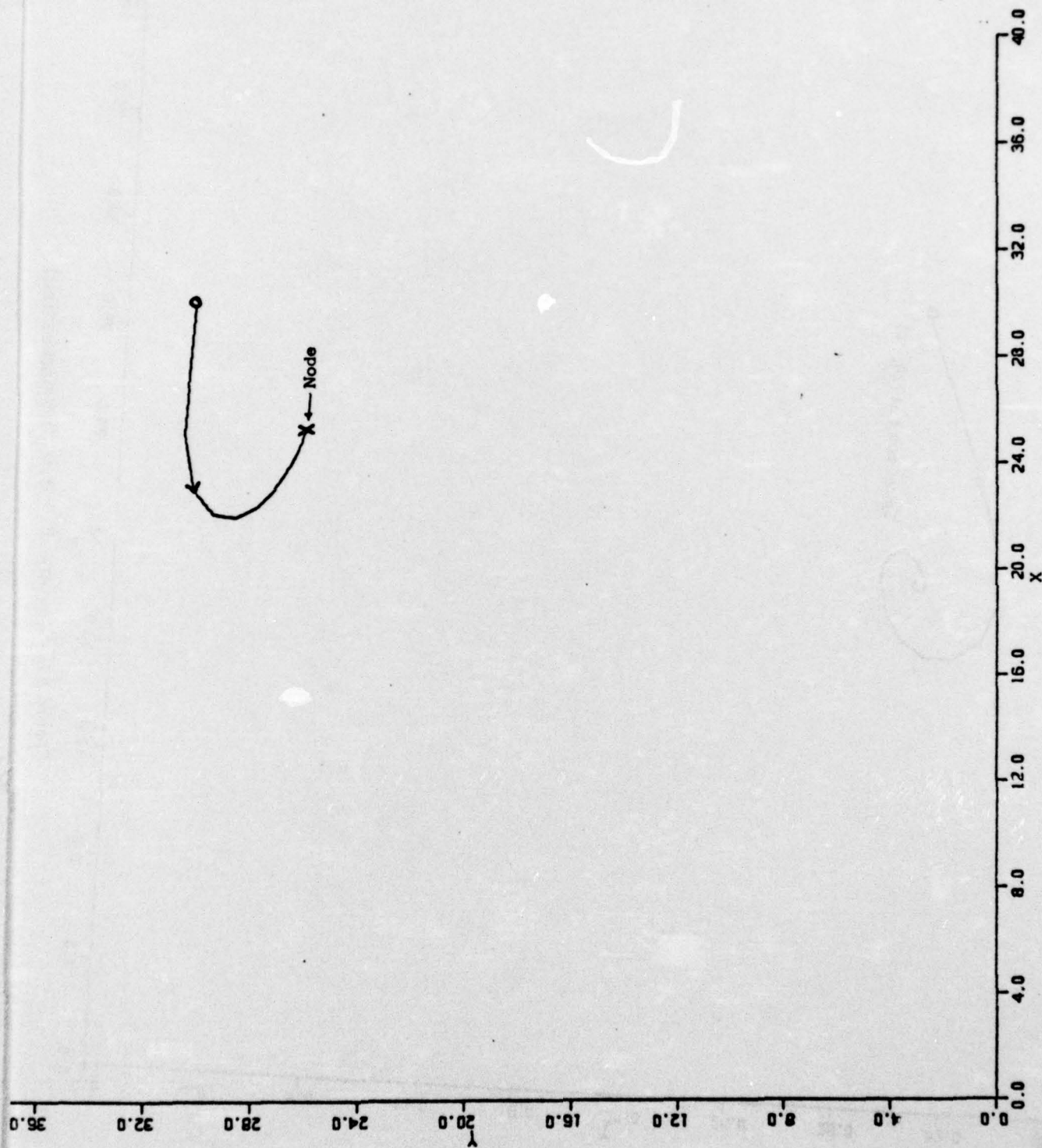


Figure 17  $K = 40$ ,  $E = 0.05$  (transition of spiral point to node)



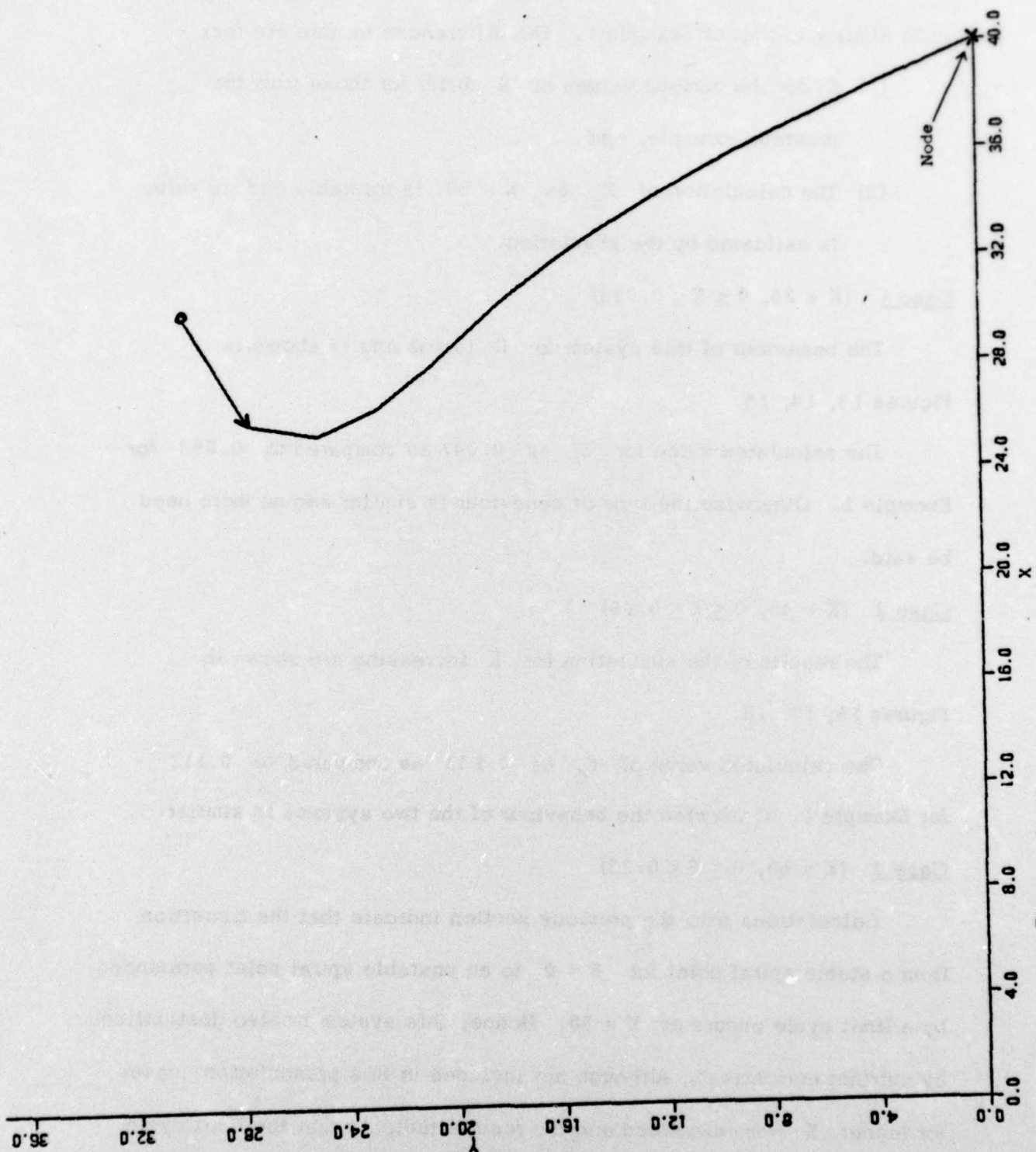


Figure 18  $K = 40$ ,  $E = 0.15$  (harvesting to predator extinction)

Although different in formulation, the behaviour of this system is quite similar to that of Example 1. The differences to note are that

- (1)  $E_c$  for the various values of  $K$  differ from those from the previous example, and
- (2) The calculation of  $E_s$  for  $K = 60$  is tractable and its value is validated by the simulation.

Case 1 ( $K = 25, 0 \leq E \leq 0.055$ )

The behaviour of this system for  $E$  increasing is shown in Figures 13, 14, 15.

The calculated value for  $E_c$  is 0.047 as compared to 0.053 for Example 1. Otherwise the type of behaviour is similar and no more need be said.

Case 2 ( $K = 40, 0 \leq E \leq 0.15$ )

The results of the simulation for  $E$  increasing are shown in Figures 16, 17, 18.

The calculated value of  $E_c$  is 0.133 as compared to 0.117 for Example 1. Otherwise the behaviour of the two systems is similar.

Case 3 ( $K = 60, 0 \leq E \leq 0.22$ )

Calculations from the previous section indicate that the transition from a stable spiral point for  $E = 0$  to an unstable spiral point surrounded by a limit cycle occurs at  $K = 50$ . Hence, this system is also destabilized by nutrient enrichment. Although not included in this presentation, cases for higher  $K$  were examined and the results indicate that the limit cycle

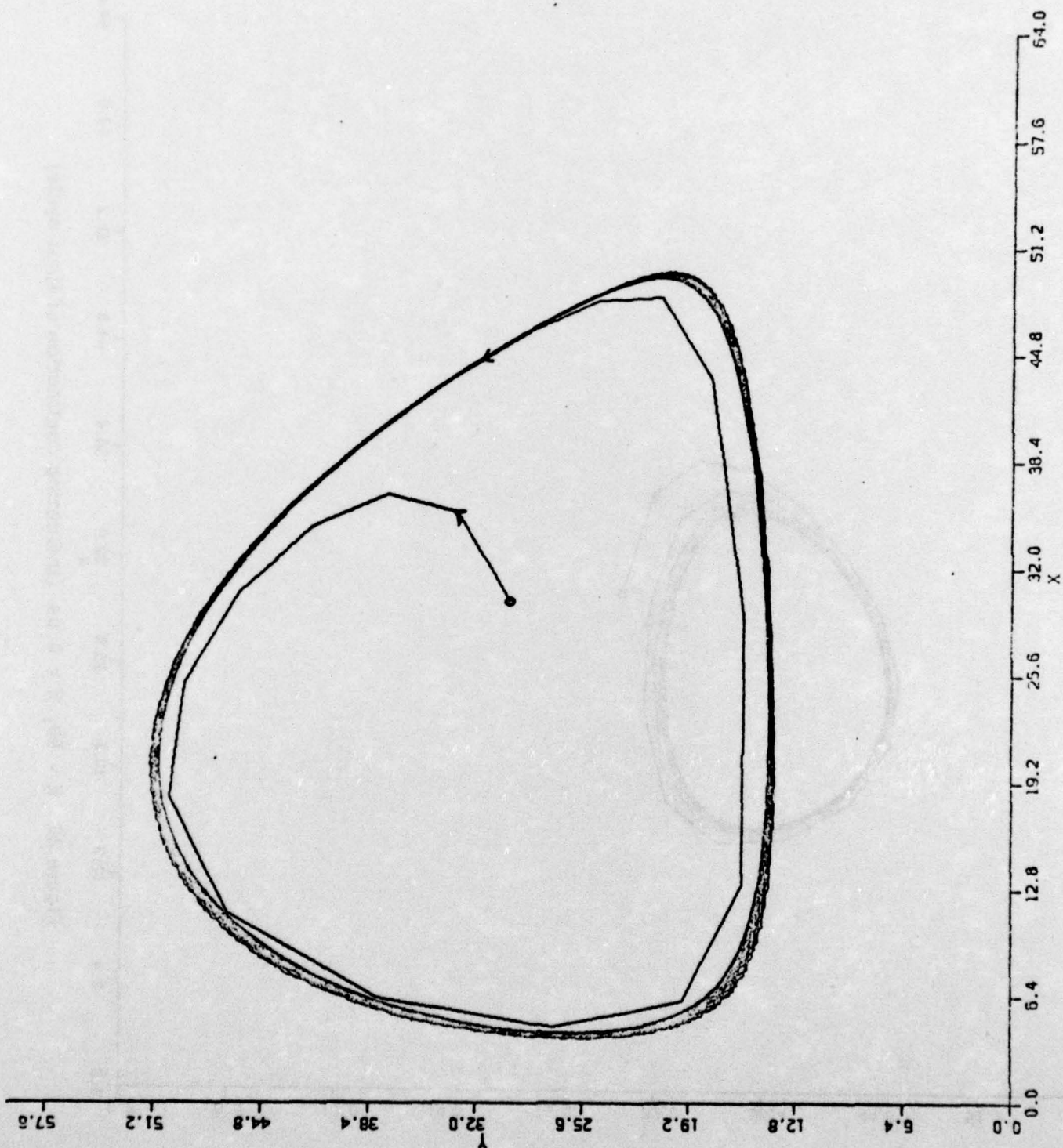


Figure 19  $K = 60$ ,  $E = 0.0$  (no harvesting)



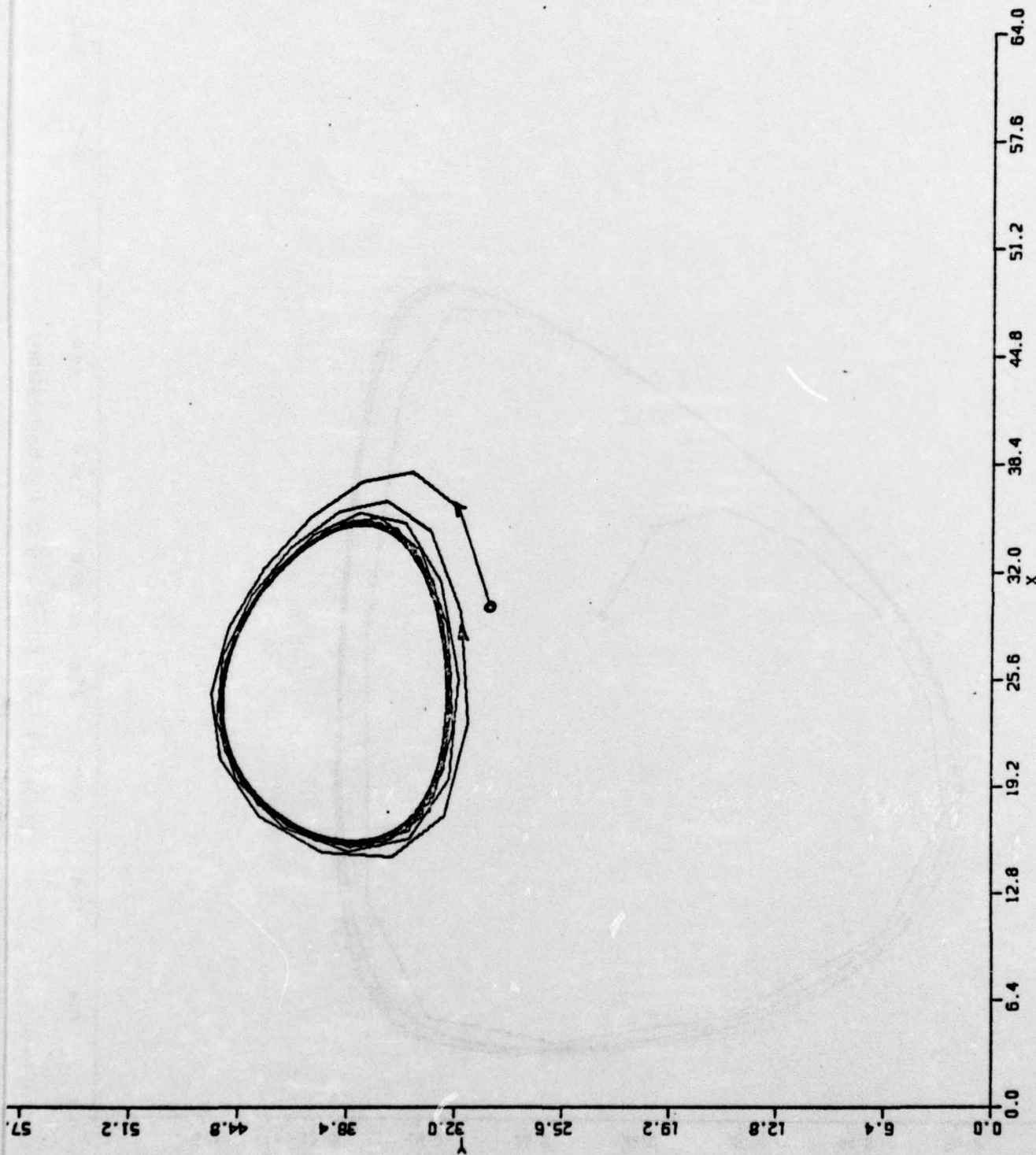


Figure 20  $K = 60$ ,  $E = 0.04$  (indicating contraction of limit cycle)

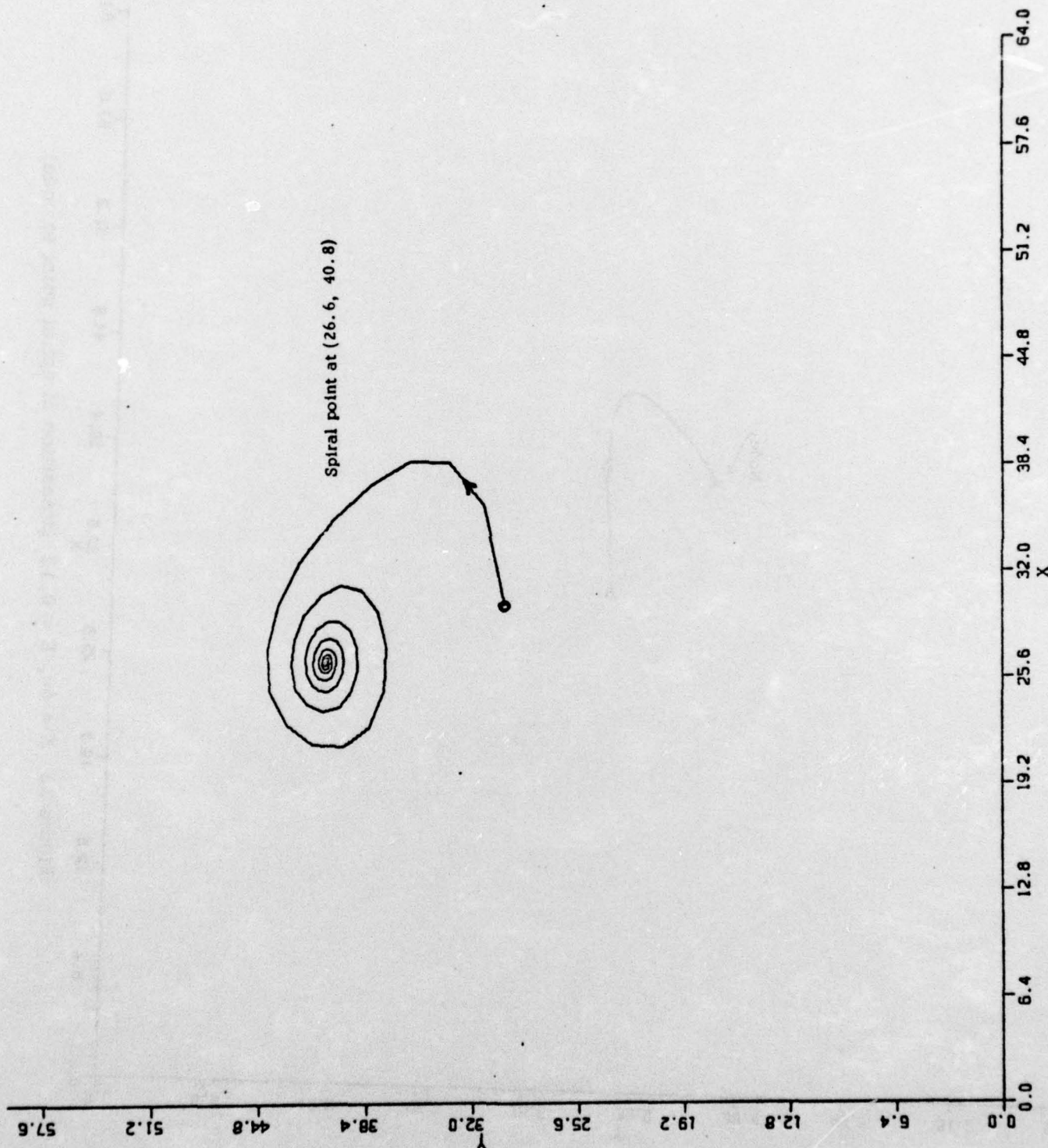


Figure 21  $K = 60$ ,  $E = 0.06$  (transition of limit cycle to spiral point)

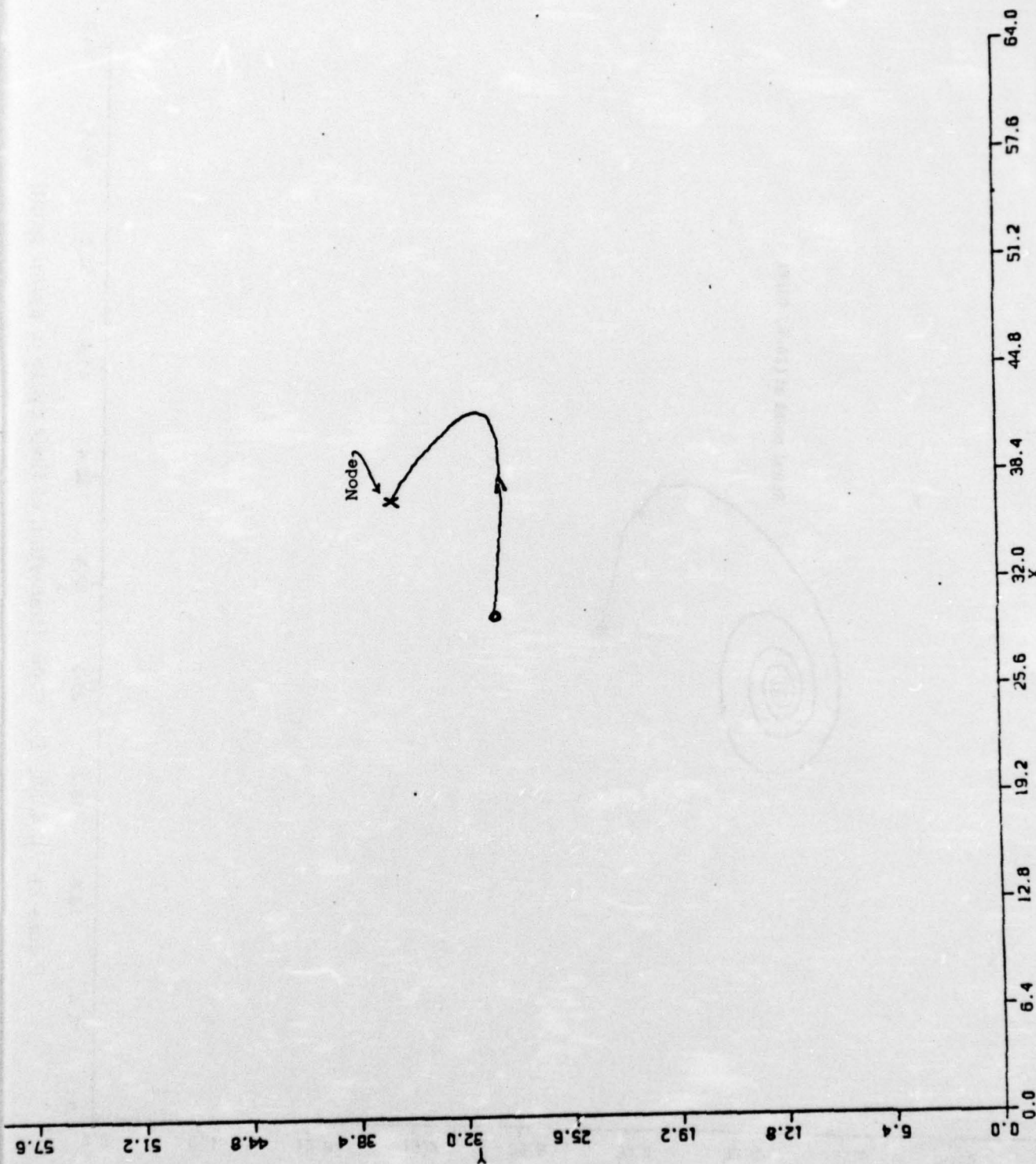


Figure 22  $K = 60$ ,  $E = 0.12$  (transition of spiral point to node)



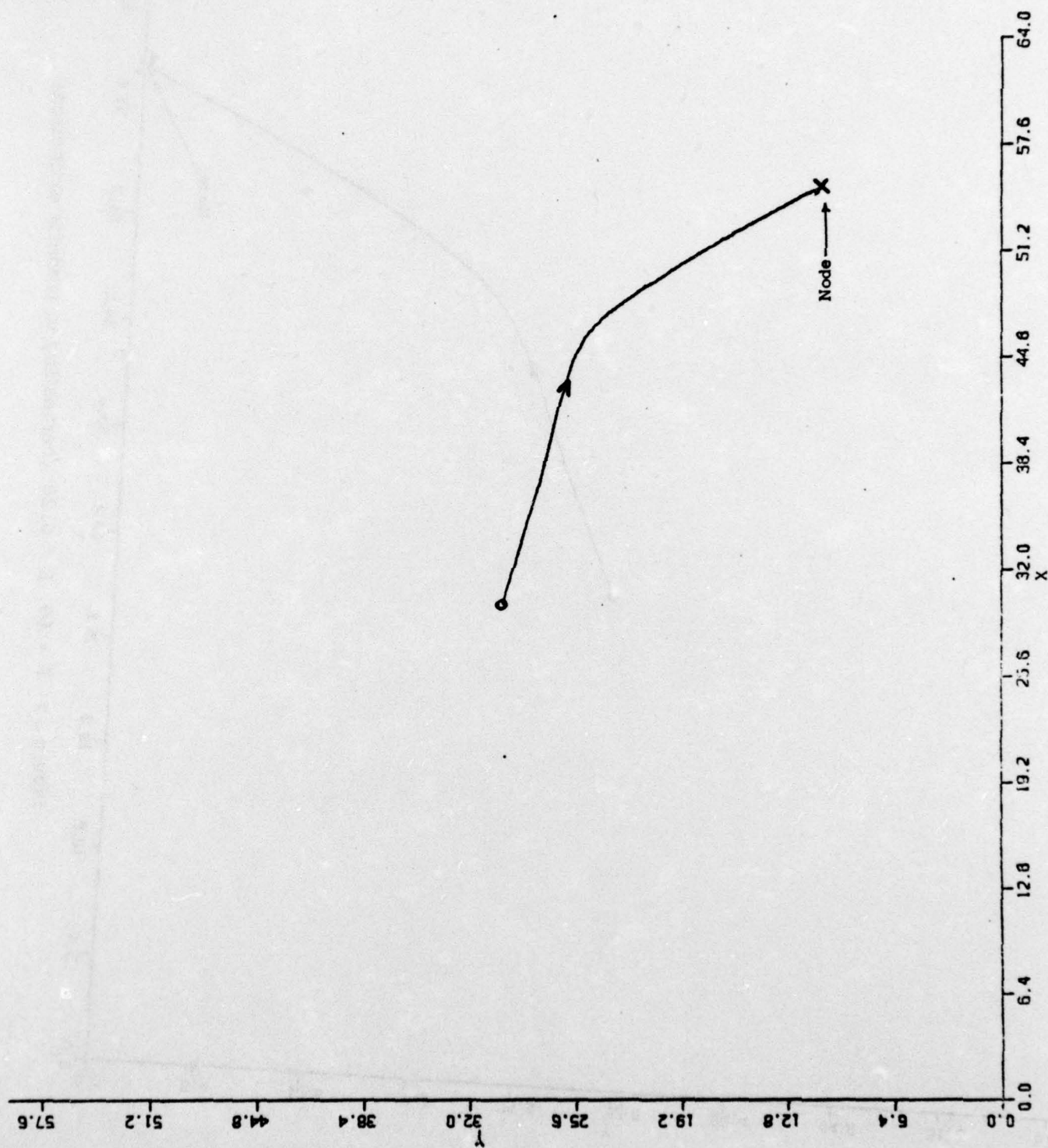


Figure 23  $K = 60$ ,  $E = 0.18$  (indicating approach of node to x-axis)

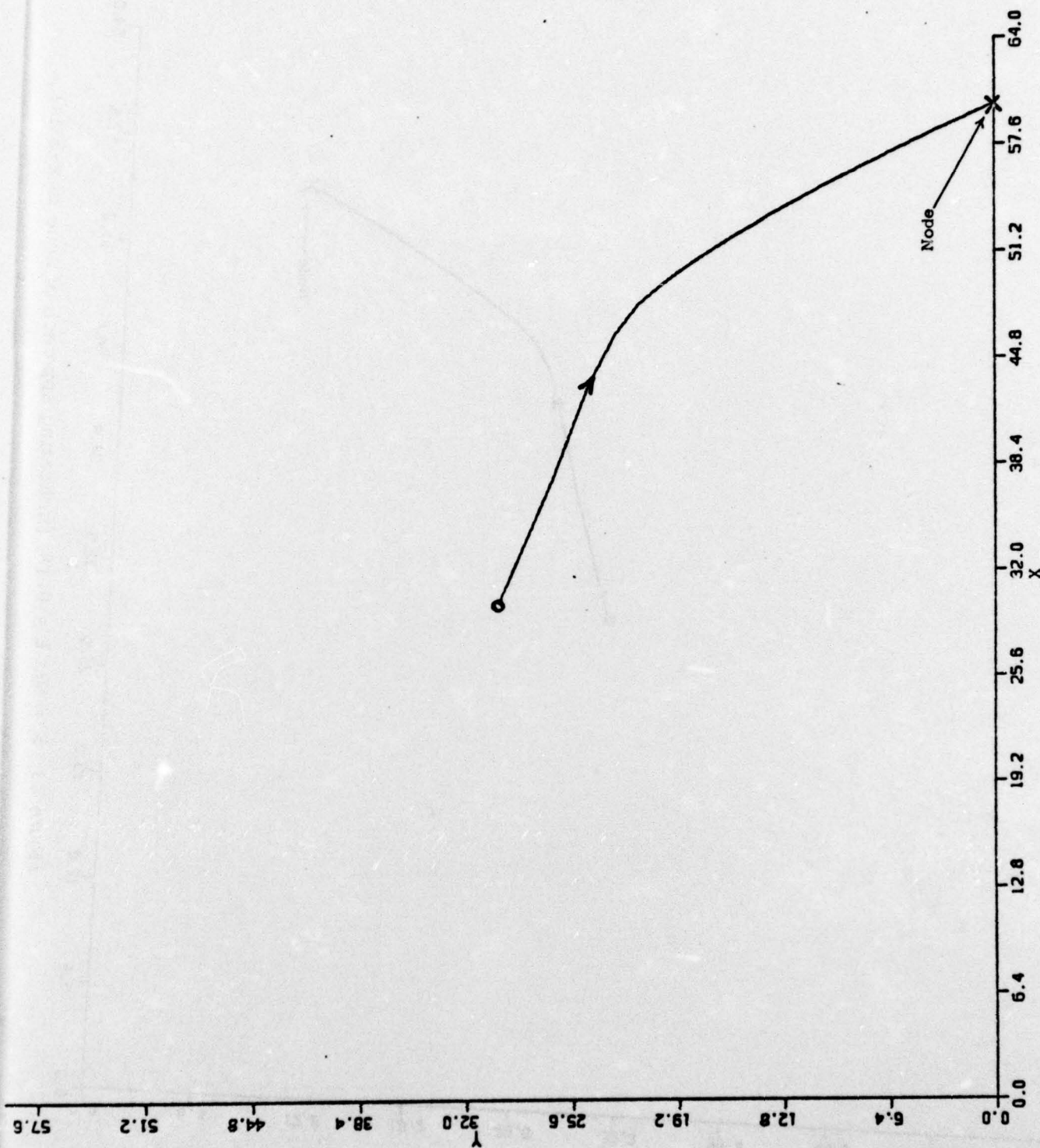


Figure 23  $K = 60$ ,  $E = 0.20$  (harvesting to predator extinction)

for  $E = 0$  comes dangerously close to the axes. Invoking the concept of practical stability therefore limits the upper value of  $K$ , and hence the intuitive conclusion that increasing prey nutrient leads to a higher predator harvest has its limitations.

The results for  $E$  increasing are shown in Figures 19 to 24.

This set of figures clearly shows the stabilizing effect of harvesting. Contraction of the limit cycle under a light harvest effort is desirable in enhancing practical stability. The calculated value of  $E_s$  (the harvesting effort to transform the unstable equilibrium to a stable one) is 0.048, and this is validated by the figures. For higher harvest rates, the equilibrium point becomes a node and approaches the x-axis. The calculated value of  $E_c$  is 0.19, which is also validated by this study.

It is worth noting that critical harvesting efforts depend on the model chosen to represent a system. The foregoing examples indicate that since more than one model might be assumed to represent the same system, care must be exercised in using the calculated value of  $E_c$  as a measure of the true system  $E_c$ .



## 5. COMPARISONS BETWEEN CONSTANT-RATE AND PROPORTIONAL HARVESTING

Comparison of the results obtained from this study to those obtained in the case of constant rate harvesting leads to the following observations:

1. In both cases, nutrient enrichment allows for higher harvest rates and efforts.
2. In both cases, the concept of "practical stability" must be invoked to prevent limit cycles from approaching the axes and to prevent the trajectory due to high harvest rates and efforts from approaching the x-axis.
3. Constant rate harvesting can produce extinction (both mathematically and biologically) of the predator in finite time. In the case of proportional harvesting, the equilibrium reaches the point  $(K, 0)$  for  $E = E_C$  and stays there. Therefore, mathematical extinction of the predators occurs only as  $t \rightarrow \infty$ . For all practical purposes, biological extinction occurs for  $E = E_C$ .
4. The high extinction sensitivity observed in constant rate harvesting is not present in proportional harvesting. Thus, proportional harvesting appears to be a safer technique. Ample warning is given that dangerous levels of harvesting are being approached, which is not the case for constant rate harvesting.

## 6. CONCLUSIONS

The object of this study was to extend the qualitative and quantitative insights obtained for constant-rate harvesting (Brauer, Soudack, and Jarosch, 1976) to predator-prey systems subjected to proportional harvesting. The results indicate that proportional harvesting is a safer method if extinction of the predator species is to be avoided.

Various intriguing questions arose during the work. For example, what type of harvesting creates a better yield? What types of strategies will improve the yield? What happens if a "closed season" is imposed on the system?

We propose to investigate these questions, the answers to which should provide a useful tool in resource management....

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UNCLASSIFIED

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER 1664	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) RESPONSE OF PREDATOR-PREY SYSTEMS TO NUTRIENT ENRICHMENT AND PROPORTIONAL HARVESTING		5. TYPE OF REPORT & PERIOD COVERED Summary Report - no specific reporting period
7. AUTHOR(s) F. Brauer and A. C. Soudack		6. PERFORMING ORG. REPORT NUMBER
9. PERFORMING ORGANIZATION NAME AND ADDRESS Mathematics Research Center, University of 610 Walnut Street Wisconsin Madison, Wisconsin 53706		8. CONTRACT OR GRANT NUMBER(s) DAAG29-75-C-0024 67-3138
11. CONTROLLING OFFICE NAME AND ADDRESS See Item 18 below.		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		12. REPORT DATE August 1976
		13. NUMBER OF PAGES 44
		15. SECURITY CLASS. (of this report) UNCLASSIFIED
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
16. DISTRIBUTION STATEMENT (of this Report)  Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES U. S. Army Research Office P. O. Box 12211 Research Triangle Park North Carolina 27709 National Research Council of Canada Ottawa, Canada		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Ecological Modelling Predator Prey Systems Stability Ordinary Nonlinear Differential Equations Harvesting of Predator-Prey Systems Computer Simulation		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) A predator-prey system is modelled by a pair of ordinary differential equations, and the qualitative effects of prey nutrient enrichment and predator harvesting at a rate proportional to the predator population size are studied. Some theoretical analysis concerning the stability of equilibrium points and the existence of stable limit cycles is included. Three models are examined as		

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cont.

20. ABSTRACT (Cont'd.)

→ examples, and for two of them computer simulations are included to illustrate the changes in qualitative behaviour under nutrient enrichment and increase of harvesting effort. The essential difference between this study and our previous work on constant rate harvesting (Brauer, Soudack, and Jarosch, 1976) is that here, extinction of predators in finite time is impossible although the predator population may tend to zero as  $t \rightarrow \infty$ . Also extinction of predators is much less sensitive to changes of harvesting effort than for constant rate harvesting.

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yields infinity.